THE RELATIONSHIPS OF THE SEA-DUCKS

(TRIBE MERGINI)

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Abstract

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This study is essentially a taxonomic analysis of the 20 species of sea-ducks which were grouped in the Tribe Mergini by Delacour and Mayr (The Family Anatidae, Wilson Bulletin, 1945, 57:1-55); it is primarily concerned with the question of the validity of the Mergini as a natural group and a determination of the most natural limits of the various genera of Mergini. The Tribe Mergini includes the eiders, Harlequin Duck, scoters, Old-squaw, golden-eyes, and mergansers. In this study I have considered evidence from 1) the structure of the trachea and tracheal bulla, 2) the plumage patterns of the downy young, 3) the plumage patterns of the adults, 4) skeletal proportions of adults, 5) variations in the diving adaptation.

The conclusions on the interrelationships of the eiders, Harlequin, Old-squaw, golden-eyes, scoters, and mergansers are based mainly on the first three of the above-named characters. In terms of these three sets of characters, the eiders have no close relationship with the scoter-golden-eye - merganser group, and the relationship of the Harlequin with either group is not clear. The data on skeletal proportions do not supply unequivocal evidence for the monophyletic origin of the scoter - golden-eye - merganser group, nor do they offer convincing proof that the eiders are or are not related to the scoters, golden-eyes, and mergansers. However, considered in conjunction with evidence from the structure of the trachea and tracheal bulla and with evidence from plumage patterns, the data on skeletal proportions have been interpreted by me in a way that sheds considerable light on the adaptive evolution that may have taken place

within the scoter - golden-eye - merganser group and within the eider group. This interpretation is further clarified when observations on the diving, feeding, and nesting habits of the species are considered.

The Tribe "Mergini" of Delacour and Mayr does not appear to be taxonomically valid. The evidence indicates that it consists of at least two unrelated groups of birds, some members of which have independently evolved similar diving adaptations. However, the results of this study support Delacour and Mayr's contentions that the golden-eyes and mergansers are very closely related and that only a single genus of mergansers (Mergus) and a single genus of scoters (Melanitta) should be recognized. Delacour and Mayr advocate recognizing only a single genus of eiders (Somateria); the results of this study indicate that two genera (Somateria and Polysticta) should be recognized.

PREFACE

This study is basically an evaluation of Delacour and Mayr's (1945) classification of the sea-ducks (Family Anatidae: Tribe Mergini); for practical reasons it is limited to treatment of a small number of the attributes of these birds, principally those which have been suggested by Delacour and Mayr in their revision of the Family Anatidae. Because a definitive statement of the relationships of the members of the Tribe Mergini must await a thorough re-examination of the rest of the Family Anatidae and a detailed study of much more evidence, my taxonomic conclusions are necessarily tentative.

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I. INTRODUCTION

The ducks, geese, and swans -- comprising the Family Anatidae -- are among the best known of all birds. Because of their edibility, beauty, and sporting value they have attracted attention from the earliest times. The Family Anatidae probably has a larger literature than any other group of birds. Phillips' bibliography (1926:321-447) comprises 2,770 titles; Kuroda's (1942), which supplements Phillips' and covers the literature through 1940, includes 6,565 titles.

It is surprising, considering their popularity, that the Anatidae have fared no better than other groups of birds with respect to their classification. There is today no general agreement on the relationships within the group. Although most authors seem to agree that the group is monophyletic and should be placed in a single suborder, one worker (Verheyen, 1953) takes another view and divides the group among four suborders (all, however, in the Order Anseriformes). The ducks, geese, and swans most frequently have been placed in a single family (Peters, Delacour and Mayr, Scott); but they have also been divided between two families (von Boetticher, 1952), and among as many as fifteen families (Verheyen).

Table 1. A comparison of several classifications of ducks, geese, and swans.

Order Anseriformes*

	Sub-orders	Families	Sub-families	Tribes	Genera	Species
Peters	1	1	10	0	62	167
Delacour and Mayr		1	2	9	40	144
Scott	1	1	3	10	40	146
von Boetticher		2	2	9**	42	143
Verheyen***	4	15	0	20	-	-

*Anhimidae and Phoenicopteridae not included.

**von Boetticher also lists 20 "sektions," a category between the genus and the tribe.

***Number of genera and species probably similar to those in Peters.

Among the recent classifications, those of Peters (1931), Delacour and Mayr (as modified by Scott, 1948-1949), and Verheyen (1953) represent the three major arrangements. The differences in the general organization of these three classifications is clear from Table 1.

I feel that the evolutionary history of the ducks, geese, and swans makes them especially difficult to work with taxonomically. With few exceptions, each of the species within the group is principally aquatic in adaptations: nesting occurs near water and young birds are taken to water soon after hatching; aquatic foods (animal and plant) form much of the diet of most species and the entire diet of many others -- very few species are entirely independent of the water for food;

the courtship of most of the species takes place on the water. The whole group is characterized by structural features which reflect dependence on water. The few terrestrial forms show only modifications of fundamentally aquatic adaptations so that it is reasonable to assume that the ancestral adaptation of the whole group is basically aquatic.

The ducks, geese, and swans form an ancient group which has been in existence since the early Cenozoic and very probably since the Upper Cretaceous. The basic aquatic adaptation of the group has undoubtedly limited the extent of the morphological and behavioral differentiation which has taken place. The evolutionary limitations of the aquatic adaptation combined with the great age of the group lead me to believe that its evolution must have involved a great deal of parallelism and convergence.

In 1945, Delacour and Mayr published "The Family Anatidae," in which they presented a new classification of the duck family. Their classification "attempts to do two things: to arrange the species in related groups and in a natural sequence, and to adjust the nomenclature of the species and genera to progressive concepts of these categories" (Delacour and Mayr, 1945:6). One of several noteworthy features of their classification scheme is the distribution of the various genera and species in new subgroups (subfamilies and tribes). One of these, the Tribe Mergini (which includes the eiders, scoters, mergansers, golden-eyes, Old-squaw, Harlequin, and Labrador ducks), is a particularly favorable group on which

to begin a study of the classification of the Family Anatidae for the following reasons:

1. All of the genera recognized by Delacour and Mayr are -- or were (*Camptorhynchus* is extinct) -- represented in the North American avifauna. Of the twenty species in the Tribe, fifteen occur in North America, and one (the Labrador Duck, *Camptorhynchus labradorius*) formerly occurred there.

2. The collections of the University of Michigan Museum of Zoology have anatomical specimens of sixteen of the species and osteological specimens of seventeen of them. Additional material is available in other museums in the United States and Europe.

3. I have been able to observe and collect personally all of the existing North American species of Mergini except Barrow's Golden-eye (*Bucephala islandica*).

The principal new features of Delacour and Mayr's classification of the group they call the Mergini are:

1. It brings together representatives from two of Peters' subfamilies (Nyrocinae and Merginae).

2. The rank of the group is reduced from subfamily to tribe level.

3. Five genera (*Arctonetta*, *Lophodytes*, *Mergellus*, *Oidemia*, *Polysticta*) are eliminated, having been merged with other genera.

A diagrammatic comparison of the two classifications (as they apply to the Tribe Mergini) is presented in Figure 1.

There are three questions that can be asked about Delacour and Mayr's Tribe Mergini:

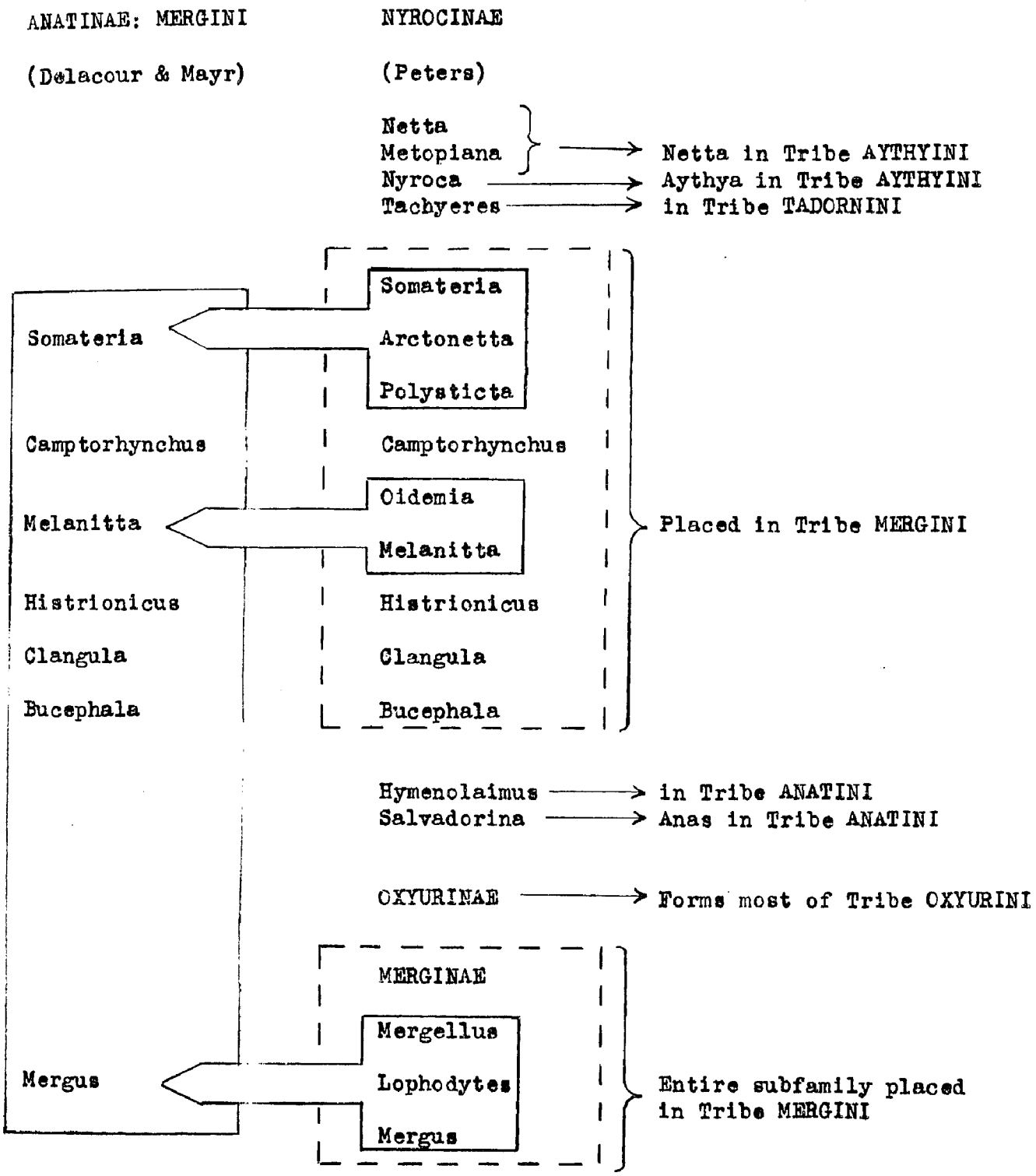


Figure 1. Comparison of the classifications of Peters (1931) and Delacour and Mayr (1945) as they pertain to the Tribe Mergini.

1. Is the Tribe Mergini a monophyletic group?

2. In the classification of the family as a whole, is a change in taxonomic rank of a major group (subfamily to tribe) warranted?

3. Are the generic mergers (with the consequent elimination of five genera) justified?

My study is primarily concerned with the question of the validity of the Mergini as a group and the validity of the various generic mergers instituted by Delacour and Mayr. The taxonomic rank of the Mergini is a corollary question which can be discussed only if the group is shown to be valid. Furthermore, assuming for the moment that the Tribe Mergini is a valid group, a discussion of its taxonomic rank would require a treatment of the whole family, which is beyond the scope of the present study.

II. CHARACTERIZATION OF TRIBE MERGINI

A. Delacour and Mayr's Evidence

Delacour and Mayr (1945:32) state that "in spite of the wide difference between the extreme forms of the tribe (*Mergus* and *Somateria*), the sea ducks [Mergini] form one of the most closely knit subdivisions of the anatine subfamily." Before attempting to evaluate the Tribe Mergini, I feel that I should present a detailed summary of the characters of the Tribe and a discussion of the evidence on which Delacour and Mayr base the validity of the Tribe. Their evidence is drawn largely from two sources:

1. Anatomy
    a. Plumage patterns
    b. Molts
    c. Trachea
2. Behavior
    a. Courtship
    b. Voice
    c. Locomotion
    d. Nesting
    e. Food habits
    f. Habitat

Delacour and Mayr's interpretation of the evidence makes it easy to see that "the seven genera are connected with one another by intermediate species" (Delacour and Mayr, 1945:32). Before listing the general characters by which

these authors have characterized the Tribe, I shall discuss their evidence for the relationships within the Tribe.

Delacour and Mayr describe the relationships between the genera as follows: "the Hooded Merganser (Mergus cucullatus)... connects the larger mergansers, through the Smew ('Mergellus' albellus) and the Buffle-head (Bucephala albeola) to the golden-eyes. The Harlequin (Histrionicus) is a link between the Old-squaw (Clangula) and the scoters (Melanitta), as is the Labrador Duck (Camptorhynchus) between the Old-squaw and the eiders (Somateria)" (Delacour and Mayr, 1945:32) (See Figure 2).

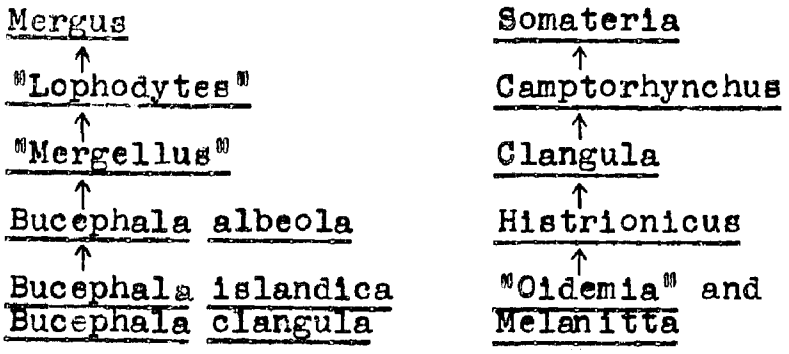


Figure 2. Relationships of the genera of Mergini.

Delacour and Mayr (1945:32) go on to say that "the golden-eyes, the Old-squaw, and the Harlequin are undoubtedly related, as is proved by the same bold pattern of dark gray and white of all their downy young. The downy young of the White-winged Scoter (Melanitta fusca) is also very similar and thus connects the whole group to the other species of the genus (M. perspicillata and "Oidemia" nigra). In turn, the downy young of the last two species link them to the eiders, all being brown above, white underneath, without strong markings. Also, immature Surf (perspicillata) and White-winged Scoters closely resemble

immature Harlequins in their general color as well as in their white head markings, which are already suggested by the white patch on the sides of the head of the Buffle-head." Using this same line of reasoning, Delacour and Mayr (1945:35) have the following to say about the relationship between the golden-eyes and the mergansers: "the downy young [of the mergansers] are dark brown above, white below, with a bold pattern resembling that of the golden-eyes, but they have a rusty tinge on the sides of the head, except in the Smew." Delacour and Mayr present other evidence for the relationship of the golden-eyes and mergansers as follows: "unlike all other ducks, mergansers are adapted to the chase of moving prey. Their body is more streamlined than that of their nearest relatives, the golden-eyes. This difference in form is particularly apparent in the sternum. In this connection also, the Smew and the Hooded Merganser seem to be somewhat intermediate between the more typical mergansers and the golden-eyes" (Delacour and Mayr, 1945:35). "In fact, except for the shape of the bill, the golden-eyes are exceedingly close to Mergus. Female Common Golden-eyes (clangula) and Barrow's Golden-eyes (islandica) resemble female mergansers closely in general color pattern; and their downy young are like those of the mergansers except that the black cap extends below the eye and the cheeks are pure white. Hybrids between Bucephala clangula on one side, and Mergus albellus (Smew) and M. cucullatus (Hooded Merganser) on the other side, have been found repeatedly in the wild state, indicating the close affinity of the golden-eyes and mergansers. The syrinx in

the two genera, with large bullae, and the inflated bulbs of the trachea, are additional proof of this relationship. The Smew lacks the enlargement of the trachea and has a smaller bulla" (Delacour and Mayr, 1945:34). "The courtship displays of the males [golden-eyes] are very elaborate, but on the whole very much like those of the mergansers..." (Delacour and Mayr, 1945:34).

Delacour and Mayr (1945:33) suggest that "the extinct Labrador Duck (Camptorhynchus) seems to be about halfway between the eiders and the eiders and the Old-squaw."

"The genera Clangula...and Histrionicus...occupy a central position among the sea ducks. They lead to the scoters and eiders on one side and to the golden-eyes and mergansers on the other" (Delacour and Mayr, 1945:34).

Delacour and Mayr consider that the golden-eyes and mergansers are related and that the eiders, scoters, Old-squaw, Harlequin, and Labrador Duck are related (see Figure 3). These relationships are supported by the plumage patterns of the downy young (and some of the immature and female plumages). Similarities in the patterns of the downy young suggest that the golden-eye-merganser group is related to the eider-scoter group through the Old-squaw and the Harlequin.

So far, I have discussed none of Delacour and Mayr's general evidence for the validity of the Tribe Mergini. Their discussion of the intergeneric relationships within the Tribe is further supported by their characterization of the Tribe as a whole. Following is a summary of the characters

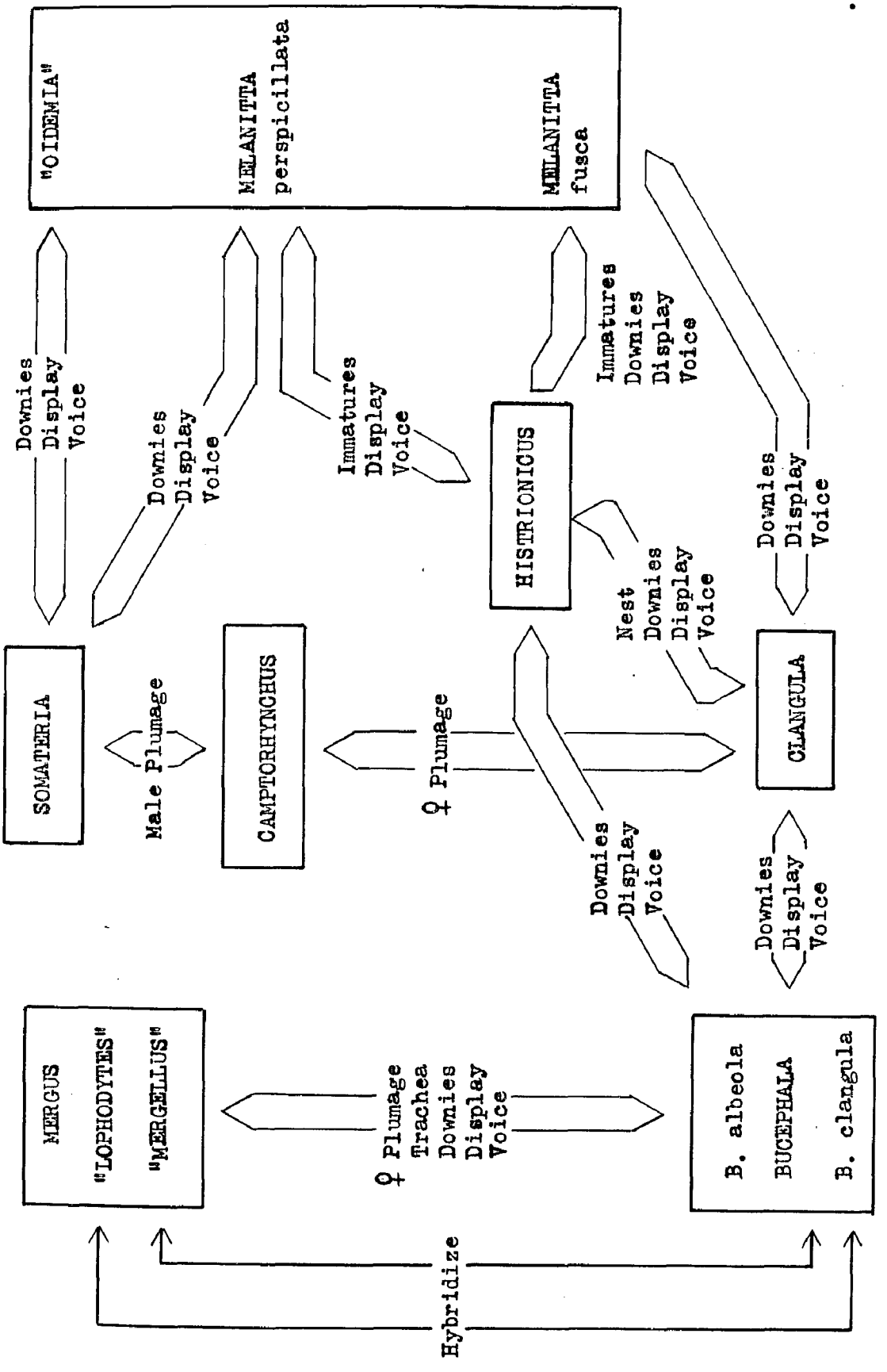


Figure 3. Relationships within the Tribe Mergini.

Delacour and Mayr consider common to all the genera of Mergini.

Plumage.-- Delacour and Mayr mention several plumage characters which they find common to all or most of the members of the Tribe:

1. "All male Mergini are brightly colored... the scoters, which are prevailingly black, and the two dull-colored southern [hemisphere] mergansers being exceptions" (Delacour and Mayr, 1945:33).

2. "There is no metallic color in the beautiful plumage of the drakes, not even in the speculum" (Delacour and Mayr, 1945:33).

3. "Iridescent gloss occurs only on the head of the golden-eyes and mergansers and on the speculum of Steller's Eiders" (Delacour and Mayr, 1945:33).

4. "Two major plumage patterns are found among the downy young of this family [=Tribe]. The eiders (Somateria) have a simplified plumage, dull gray-brown above with white breast and belly. Common and Surf Scoters are similar, but more blackish, with an indication of white cheeks and of a dark cap. The White-winged Scoter, Old-squaw, and Harlequin lead to the typical Bucephala pattern. It is boldly black and white. A blackish cap, extending to a line well below the eye, contrasts with the white cheeks. The ulnar edge of the wings and two or three lateral spots on the back are white. The mergansers (Mergus) are essentially similar, except that the sides of the face are washed with rufous. Some have a light superciliary" (Delacour and Mayr, 1945:48).

Molt.-- Delacour and Mayr's Subfamily Anatinae is characterized by the fact that all of its members have a double annual molt. This, of course, must be true of all Mergini for the Tribe to be included in the Subfamily Anatinae. Another molt character of the Mergini is that "they are not adult before their second or third year" (Delacour and Mayr, 1945:33). Furthermore, "all male Mergini...have a distinct eclipse plumage, the scoters... and the two dull-colored southern mergansers being exceptions" (Delacour and Mayr, 1945:33).

Trachea.-- Delacour and Mayr (1945:4) agree with the Heinroths (O. and M. Heinroth, 1928) that, for taxonomic purposes, one of the most important non-adaptive characters is "the structure and shape of the syrinx and trachea.... The taxonomic advantage of this structure lies in the fact that its shape is not easily modified by any peculiar adaptations of a given species. It tends to be phylogenetically conservative."

Although Delacour and Mayr have refrained from broadly characterizing the Tribe Mergini in terms of the structure of the trachea and syrinx, they state (1945:43) that "the structure of syrinx and trachea is fairly uniform within each tribe." They go on to describe a few apparently unimportant variations in the vocal apparatus of various ducks; I quote those applying to the Mergini (Delacour and Mayr, 1945:43): "in Mergus merganser and M. serrator the bulla is exceptionally large.....in two species of scoters it is very

small; in Melanitta nigra the bulla is absent. The trachea shows special bulbous inflations...particularly among the Mergini (Bucephala, some species of Mergus, Melanitta). The bronchi are elongated and inflated in Melanitta fusca and in Somateria....As with all taxonomic characters, the structure of the syrinx sometimes varies independently of the system. This is true particularly in the genera Cygnus, Tadorna, Melanitta, and Mergus. Differences in the structure of the syrinx occur in these genera at the species or even at the subspecies level."

Courtship and voice.-- "The sea ducks generally have very elaborate displays which have little resemblance to those of any other Anatinae, except perhaps to some of the postures of the stiff-tailed ducks" (Delacour and Mayr, 1945:33). "The Old-squaws, Harlequins, scoters, and eiders resemble the mergansers and golden-eyes in voice as well as in display, though the display is simpler, consisting of stretching the neck and calling, with an upward jerk of the bill" (Delacour and Mayr, 1945:33).

"Sea ducks are very silent birds as a rule, even the females; female eiders, however, utter frequently a harsh grunting cackle. Some of the others utter a similar cackle during the breeding season; at that time, the males emit low, subdued, ventriloquial grunts or whistles, differing from species to species. The only noisy drake is the Old-squaw, which calls loudly in all seasons" (Delacour and Mayr, 1945:33). Comparing Clangula and Histrionicus, Delacour and Mayr (1945:34)

decide that "Clangula is by far the more vocal of the two, but otherwise the displays of the two genera are very similar."

Locomotion and food habits.-- "The birds of this tribe, with a very few exceptions, spend a part of their time at sea, and animal life constitutes their principal food. They are all great divers. Their bill is strong, with a large hooked nail, and varies from long, thin, and narrow to thick and short, according to their principal food (fish, mussels, etc.). Their wings are short and their flight heavy, and they walk with some difficulty, the eiders being less clumsy on land than the others" (Delacour and Mayr, 1945:32). "The mergansers (Mergus), the only ducks that have evolved into habitual fish eaters, have a long narrow bill with 'teeth especially adapted to catching this type of food. The bill seems to be the most plastic of all the morphological characters of ducks, differing strikingly even among close relatives" (Delacour and Mayr, 1945:50-51).

"Several branches, for example, the pochard group, the golden-eye - merganser - scoter group, and the stiff-tailed duck group, have developed into divers par excellence, and are structurally rather similar to one another. However, their non-adaptive characters, such as the general proportions of the body, the color pattern of the downy young, the structure of the syrinx, and the courtship performances, are sufficiently different among the three groups to suggest that the three are not at all closely related" (Delacour and Mayr, 1945:4).

Nesting.-- "The majority of the species nest in the hollows of trees, in holes and crevices in rocks, or any

other sort of deep shelter. Some of the scoters and eiders, however, deposit their eggs on the ground in the open, among grasses and bushes" (Delacour and Mayr, 1945:32-33). "All eiders are ground nesters and breed usually near the seashore, but also on the arctic tundra, near fresh-water pools" (Delacour and Mayr, 1945:33). "Both species [Clangula and Histrionicus] are ground nesters, although the Harlequin is reported to nest occasionally in holes in trees or in cliffs" (Delacour and Mayr, 1945:34). "Nothing is known of the nesting of the three rarer [mergansers]...(squamatus, australis, octosetaceus). The Red-breasted Merganser (serrator) nests on the ground among rocks and in depressions. The other three species (albellus, cucullatus, and merganser) nest by preference in tree holes" (Delacour and Mayr, 1945:34).

Delacour and Mayr (1945:50) recognize four principal types of nests in the family Anatidae. Their classification of types of nests (as it pertains to the Mergini) follows: "(a) open nests on the ground, the prevailing type of nest in all tribes of ducks, except the Cairinini and Mergini; (b) open nests raised above the ground (on rocky ledges, tree stumps, old nest of other birds)... [no Mergini listed]; (c) concealed nests, on the ground under rocks, or in holes in the ground, found in...Mergini (Somateria, Melanitta, usually Histrionicus, Clangula, Bucephala islandica, Mergus serrator and ?M. australis); (d) holes in trees, found in... Mergini (most species of Mergus, Bucephala, sometimes Histrionicus)."

B. Anatomical Considerations

In studying the relationships within a group of animals it is theoretically possible to find useful taxonomic characters in each of the anatomical systems. In actual practice the systematist must limit himself to a consideration of those sources of evidence which promise to be the most fruitful. In this study I have used evidence from 1) the structure of the trachea and tracheal bulla, 2) the plumage patterns of the downy young, 3) the plumage patterns of the adults, 4) skeletal proportions, 5) variations in the diving adaptation. The first three of these topics will be treated in this section in an attempt to shed light on the validity of the Tribe Mergini. All of the topics will be treated in more detail in Chapters III and IV.

Trachea.-- Various authors, notably the Heinroths (1928) and Delacour and Mayr, have commented on the value of the trachea as a source of evidence for the classification of ducks. It is noteworthy that a close examination of this structure in the Mergini suggests a taxonomic arrangement entirely different from that proposed by Delacour and Mayr.

The trachea is a long tube of cartilaginous or bony rings. One end of the tube leads to the mouth cavity by way of the larynx and the glottis; the other end of the tube gives rise to two bronchial tubes which lead to the lungs. The males of many species of ducks have a special structure at the end of the trachea which gives rise to the two bronchi. This structure is called the tracheal bulla. The tracheal bulla of the

Anatidae is a modification of the lower end of the trachea; it consists of a fusion of several tracheal rings. It occurs only in males. Females (and males which lack the tracheal bulla) have a small, fused (or partially fused), bilaterally symmetrical structure at the lower end of the trachea.

Males of the different species of Mergini have four major conditions of the tracheal bulla.

In the first condition, the tracheal bulla is absent. Males which lack the tracheal bulla have a small, fused (or partially fused), bilaterally symmetrical structure at the lower end of the trachea. This structure is similar to (or identical with) the structure at the lower end of the trachea of females. In the Tribe Mergini, the Common Scoter (Oidemia nigra) is the only species the males of which lack the tracheal bulla (see Chapter III). Several other tribes, namely the Anserini, the Cygnini, and the Oxyurini are characterized by a lack of the tracheal bulla in males.

The second type of tracheal bulla is bilaterally symmetrical. The right and left chambers are enlarged and their lateral margins are dorso-ventrally compressed. Neither chamber has a bulbous appearance. The bulla is incompletely fused; laterally each of the two chambers is well fused, medially the fusion is incomplete and the basic ring structure can be distinguished. A short length of the trachea just anterior to the tracheal bulla is composed of incomplete rings; this results in a median, membrane-covered space. In the Tribe Mergini, the White-winged Scoter (Melanitta fusca) and the

Surf Scoter (Melanitta perspicillata) are characterized by this type of tracheal bulla (see Chapter III).

The third type of tracheal bulla is asymmetrical and consists of two irregular inflations -- at least one of which has one or two membrane-covered fenestrae. There is considerable interspecific variation in the superficial appearance of this type of tracheal bulla, although the basic structures are present in all the species characterized by type 3. The right chamber may be only slightly inflated or it may be greatly inflated. The amount of fusion of the right chamber is also variable; in some the basic ring structure is easily discernible, while in others fusion is so complete that no rings can be traced at all. The left chamber is also variable. It always has at least one membrane-covered fenestra and fusion is generally so complete that ring outlines are indiscernible. In the Tribe Mergini, the Golden-eyes (Bucephala clangula and islandica), Buffle-head (Bucephala albeola), Smew (Mergellus albellus), Hooded Merganser (Lophodytes cucullatus), true mergansers (Mergus), and Old-squaw (Clangula hyemalis) are characterized by this type of tracheal bulla (see Chapter III). The Tribe Aythyini, the pochards, is also characterized by this type of tracheal bulla.

The fourth type of tracheal bulla is asymmetrical and consists of a single, fairly regular, bulbous inflation which lacks any membrane-covered fenestrae. In the Tribe Mergini, the Harlequin Duck (Histrionicus) and the eiders (Somateria, Arctonetta, Polysticta) have this type of tracheal bulla (see

Chapter IV). The Wood Duck (Aix sponsa), the Falkland Flightless Steamer Duck (Tachyeres brachypterus), and the Black Duck (Anas rubripes), and other species of the genus Anas likewise have this condition of the tracheal bulla.

Within any group of ducks, such as the eiders, golden-eyes, or mergansers, the tracheal bulla may exhibit considerable interspecific variation. Nevertheless, the bulla is consistently type 4 in the case of the eiders, and type 3 in the cases of the mergansers, golden-eyes, and pochards. In the Tribe Mergini the distinction between the type-3 and type-4 tracheal bullae is a sharp one; it is not possible to set up a morphological series connecting the two types. Presumably in the evolutionary development of types 2, 3, and 4, the female-like condition of absence is the ancestral type. Types 3 and 4 appear to be the end-products, neither of them easily derived from the other. Furthermore, types 3 and 4 do not vary to the extent that either of them can be easily derived from type 1. Type 2, however, is easily derived from type 1. The fact that the scoters possess both types 1 and 2 of the tracheal bulla suggests that the type-2 bulla evolved from type-1 condition (absence of bulla).

Assuming that the lower end of the trachea of the common Scoter (Oidemia nigra) represents the ancestral condition, the scoters have made the transition from the type-1 condition of absence to the simple, bilaterally symmetrical type-2 tracheal bulla.

We cannot assume that all forms lacking the tracheal bulla represent descendants of a form or forms ancestral to

ducks with the type 2 tracheal bulla. Swans, geese, and stiff-tails all lack a tracheal bulla. However, the stiff-tails have a structure at the lower end of the trachea which is very different from that characteristic of the swans and geese and very similar to that found in the Common Scoter.

The type-2 tracheal bulla has both the right and the left chambers expanded, is incompletely fused, and has some definite shape characteristics which are comparable to shapes found in some of the type-3 tracheal bullas. These facts suggest that the type-2 bulla is a precursor of type-3.

Let us assume for the moment that the evolutionary development of the type-3 tracheal bulla passed from absence of a bulla through a stage similar to type-2. The type-4 tracheal bulla presumably also evolved from the type-1 condition of absence; however, the type-2 tracheal bulla does not supply a feasible intermediate step. The form of the trachea itself supplies additional evidence for this contention.

The tracheal tubes of males of several species of Mergini have mid-tracheal swellings -- some of them highly specialized bulbous structures and others merely slight increases in the diameter of the tube. Such mid-tracheal swellings are characteristic of all tracheas with types 2 and 3 tracheal bullas, except Bucephala albeola, Mergellus, and some species of Aythya. None of the tracheas with the type-4 tracheal bulla has any mid-tracheal swellings; all Mergini with type-4 tracheal bullas except Histrionicus have tracheal tubes of uniform diameter.

Plumage patterns.-- The eiders are at once distinguished from the other members of the Mergini by the barred, somewhat Anas-like pattern of the females. Females of the rest of the Mergini are either more or less uniform sooty brown with various head markings (scoters, Histrionicus), or are contrasting -- i.e., brown head with or without markings, and gray back contrasting with light, unmarked belly (Bucephala, Mergellus, Lophodytes, Mergus, Clangula).

The patterns of the downy young of the various species fall into two main groups -- the eiders in one and the rest of the species in the other. Downy eiders are brown and, except for Polysticta, all of them quite pale. None of them has the bold pattern characteristic of the golden-eyes, mergansers, scoters (except Oidemia and M. perspicillata), Harlequin, and Old-squaw. All of the downy Mergini except the eiders are either slaty-brown or almost black. Where the face pattern of the downy eiders consists of a faint, pale superciliary and a fine, dark line through the eye, the other downy Mergini have a white cheek-patch (entirely or in part reddish-brown in most of the mergansers) contrasting with the dark crown. This cheek-patch is clearly apparent in Oidemia and Melanitta perspicillata, both of which lack the contrasting body markings of the mergansers, golden-eyes, etc.

C. Biological Characters

Delacour and Mayr (1945:49) state that "biological characters are of paramount importance to the classifier, for

habits and behavior are certainly deeply rooted and are often the product of a very ancient evolution." Lorenz (1951:161) comments that "the taxonomic usefulness of inherited specific behavior has gradually become common property of zoological systematics..."

"Biological characters" of great importance to systematists working with the Anatidae are courtship and display behavior, nesting habits, ecological distribution, feeding habits, hybridization, and locomotor habits. Other "biological" characteristics, as yet poorly understood, are protein specificities (serology) and chromosome variations (cytogenetics).

Because of the incompleteness of our knowledge of serology and cytogenetics of the members of the Tribe Mergini, these subjects will not be treated here.

Hybrids.-- Ducks are notable for the amount of hybridization that takes place among the various species. Hybrid anatids have attracted the attention of ornithologists and aviculturists for a long time. So far, however, no one has made a satisfactory general statement of the taxonomic significance of these hybrids; nor has any one presented a satisfactory taxonomic interpretation of variations in hybrid fertility. Delacour and Mayr (1945:51) state: "it appears that the degree of fertility of hybrids is a fairly reliable clue to relationship, but its significance varies a good deal among the various groups, and there are numerous striking exceptions." Yamashina (1952) has studied the cytogenetics of the Anatidae and has related his findings to the problems of

hybrid sterility and fertility in that group. Yamashina (1952:6) states that "if the parental chromosome complexes are not identical, the conjugation of the corresponding chromosomes is more or less irregular, and when the difference between the corresponding chromosomes is too great the germ cells degenerate due to a failure of conjugation... This may be gauged by the strength of hybrid sterility..." Yamashina (1952:7-8) uses variations in hybrid fertility to delimit taxonomic categories as follows:

1. "If the hybrid between two groups of individuals shows any sterility due to dissimilarity of the parental chromosome complexes, these two groups are considered to be different species."

2. "The genus is a group of individuals whose F_1 hybrid shows at least some degree of fertility."

3. "If the hybrids between two groups of individuals show total sterility due to dissimilarity of the parental chromosome complexes, these two groups of individuals are considered to be different genera."

4. "The family is a group of those individuals which can produce an F_1 hybrid able to reach maturity....It can be stated only that the production of an adult F_1 hybrid between two groups of animals proves their confamilial relationship. Inability to produce such a hybrid does not necessarily mean they are not of the same family."

However, I do not think that chromosome structure is as taxonomically conservative as Yamashina thinks. As with other

morphological characters, modification of the structure of the chromosomes undoubtedly has taken place at different rates in different groups of animals. It is unreasonable to assume that, because the hereditary factors are borne on the chromosomes, our interpretation of genetic relationships must be based entirely on modifications of chromosome structure.

Systematists attempt to establish relationships among organisms in terms of morphological, behavioral, and other presumably inherited characteristics. The assumption made by a systematist is that the amount of similarity between two organisms is an index of their relationship with one another. A logical corollary of this assumption is that phenotypical similarity is an index of genetic similarity and that when we compare two organisms phenotypically we are by indirect means comparing their gene complements. It is reasonable to suppose that chromosomal aberrations may take place with little or no change in the gene complements of the chromosomes. In other words, if sterility is related to chromosome configuration (ignoring for the moment sterility genes) and genetic similarity is related to the gene complements of the chromosomes, hybrid sterility may develop between two animals (or not develop) regardless of the similarity of their gene complements. Furthermore, it is logical to suppose that closely related animals (in terms of their gene complements) are more likely to be karyotypically similar than distantly related animals because there has been less opportunity for genic or chromosomal

differentiation. At the same time, the fact that two animals have very different gene complements does not mean that they will be karyotypically distinct (and hence intersterile) although there is greater likelihood that this will be the case.

Evidence from hybridization is difficult to use taxonomically for the following reasons:

1. The inability of two species to produce a hybrid does not mean that they should not be placed in the same genus or other supraspecific category.

2. The production of a totally sterile hybrid does not mean that the two parent species are generically distinct.

3. The production of a fertile hybrid indicates that the parent species are probably closely related and very likely congeneric if not conspecific, depending on frequency of occurrence and degree of fertility. However, hybrid fertility is an unreliable criterion of relationship in the Anatidae because genetic sterility (due to "sterility genes") and chromosomal sterility appear to develop in this group independent of the development of other gene differences.

I have found no record that any of the following species in the scoter - golden-eye - merganser group have been involved in the production of a hybrid: Clangula hyemalis, Mergus australis, Mergus octosetaceus, Mergus squamatus. Among the eiders, Polysticta stelleri and Arctonetta fischeri have never been recorded as having hybridized with any species; there are no records of hybrids involving Histrionicus histrionicus.

Hybrids between species within the scoter - golden-eye - merganser group are as follows:

1. Melanitta fusca × Bucephala clangula. Phillips, 1926:42; Leverkühn, 1890:222; Ball, 1934:4; Poll, 1911:459; Phillips, 1925:322. Leverkühn (1890:222) lists one example of this hybrid.

2. Melanitta fusca × Melanitta perspicillata. Ball, 1934:4; Baird, Brewer, and Ridgway, 1884:100. This hybrid is described in Baird, Brewer, and Ridgway (1884:100); I do not believe they have fully verified the record. In describing the hybrid, they state (1884:100); "the differences in the markings of the head would not alone be sufficient to indicate more than a variation of plumage of the common species; but the form and coloration of the bill is so different as to suggest the possibility of the specimen being a hybrid between P. perspicillata and Melanetta fusca or velvetina. The wing, however, is said to lack the white speculum of Melanetta."

3. Bucephala clangula × Bucephala islandica. Snyder, 1953:199. One record, a male, described from a specimen.

4. Bucephala clangula × Lophodytes cucullatus. Ball, 1934:7-24; Phillips, 1926:255; Poll, 1911:462; Cockrum, 1952:143; Sibley, 1938:334. Ball (1934) describes two examples of this hybrid; I know of no others.

5. Bucephala clangula × Mergellus albellus. Ball, 1934:4,5; Phillips, 1926:240; Poll, 1911:462; Leverkühn, 1890:222; Lundin, 1954:180-182, 196. Leverkühn (1890:222) lists five examples of this hybrid; Ball (1934:4) also lists five, probably the same examples. Lundin (1954:180-182) lists

and figures four male hybrids between the Common Golden-eye and the Smew. Comparison of Lundin's and Leverkühn's records reveals that they are all different.

6. Bucephala clangula × Mergus merganser. Sibley, 1938:334; Phillips, 1926:277; Ball, 1934:4; Poll, 1911:462; Leverkühn, 1890:226. According to Leverkühn (1890:226) "several" examples of this hybrid have been described.

7. Lophodytes cucullatus × Mergus serrator. Erickson, 1952:167. This hybrid is known only from a "sight record".

Hybrids between species in the scoter - golden-eye - merganser group and other species are as follows:

1. Oidemia nigra × Anas penelope. Phillips, 1926:24; Poll, 1911:461; Leverkühn, 1890:230. Leverkühn (1890:230) lists one example of this hybrid.

2. Bucephala clangula × Aythya marila. Ball, 1934:4; Phillips, 1925:322; Poll, 1911:459; Leverkühn, 1890:222. Leverkühn (1890:222) lists one example of this hybrid; Ball (1934:4) lists two examples, one of which is possibly that mentioned in Leverkühn.

3. Bucephala clangula × Aythya ferina. Phillips, 1925:322; Poll, 1911:458; Ball, 1934:4; Leverkühn, 1890:222. Leverkühn (1890:222) and Ball (1934:4) each list one example of this hybrid.

4. Bucephala clangula × Aythya nyroca. Sibley, 1938:334.

5. Bucephala clangula × Aythya fuligula. Phillips, 1925:322; Astley, 1921:99. Astley (1921:99) states: "I have a male Golden-eye mated to a female Tufted Duck. Last year

she successfully concealed her nest and hatched out her brood of eight or nine, but as usual all disappeared..." I do not feel that one can fairly say on that evidence that these two species have produced hybrid offspring.

6. Bucephala clangula × Anas querquedula. E. Geoffroy St. Hilaire's paper (1806) on this hybrid has the following title: "Description d'un mulet provenant du canard morillon (Anas glaucion) et de la sarcelle de la Caroline (Anas querquedula)." "Sarcelle de la Caroline" means "Carolina Teal"; one of the common names of the American Wood Duck (Aix sponsa) is Carolina Duck. I believe that a misinterpretation of common names led Yarrell (1884-1885:439) to make what is probably an erroneous statement: "G. St. Hilaire has described the hybrid offspring resulting from the union of the Golden-eye and the American Wood Duck." However, Yarrell listed no reference for Geoffroy St. Hilaire. Having been able to find but one reference by Geoffroy St. Hilaire describing a hybrid involving the Golden-eye, I am satisfied that Yarrell is in error. Phillips (1925: 322) cited Yarrell and perpetuated his error.

7. Mergus merganser × Anas platyrhynchos. Ball, 1934: 3,5-6; Phillips, 1926:277; Sibley, 1938:334; Schlüter, 1891: 109-110. Ball (1934:3,5-6) lists one example of this hybrid, the one originally described by Schlüter (1891:109-110).

8. Bucephala albeola × Aythya fuligula. Sibley, 1938:334.

Hybrids of species in the eider group are as follows:

1. Somateria mollissima × Somateria spectabilis. Phillips, 1926:110; Leverkühn, 1890:220; Cockrum, 1952:143.

According to Leverkühn (1890:220) "several" examples of this hybrid have been described.

2. Somateria mollissima X Anas platyrhynchos. Phillips, 1926:110; Clarke, 1912:198-201; Allen, 1927:275; Anon, 1912: 165; Ball, 1934:3. A note in British Birds (Anon, 1912:165) describes Clarke's (1912:198-201) observation of a male hybrid eider X mallard and mentions observation of another example. Allen (1927:275-276) describes a female-plumaged mallard X eider hybrid with curly tail coverts, a puzzling example. There are at least two well substantiated records of this cross.

The above list of seventeen hybrids (at least three of them doubtful) involving most of the species in the Tribe Mergini is difficult to interpret taxonomically. There is no information on the fertility of any of these hybrids. It is impossible to say that the above list represents all of the possible hybrid combinations involving species in the Tribe Mergini. Until more information is available about the frequency and fertility of hybrids involving Mergini I think it unwise to draw any taxonomic conclusions from this evidence. With this reservation in mind, it is interesting to note that there are in the scoter - golden-eye - merganser group over fifteen examples of hybrids of Bucephala clangula (not all different crosses) involving all but two (Clangula and Oidemia) of the genera in the group; nine of these hybrids are with Mergellus albellus. It is also noteworthy that there is only one hybrid known involving Bucephala and Anas but there are

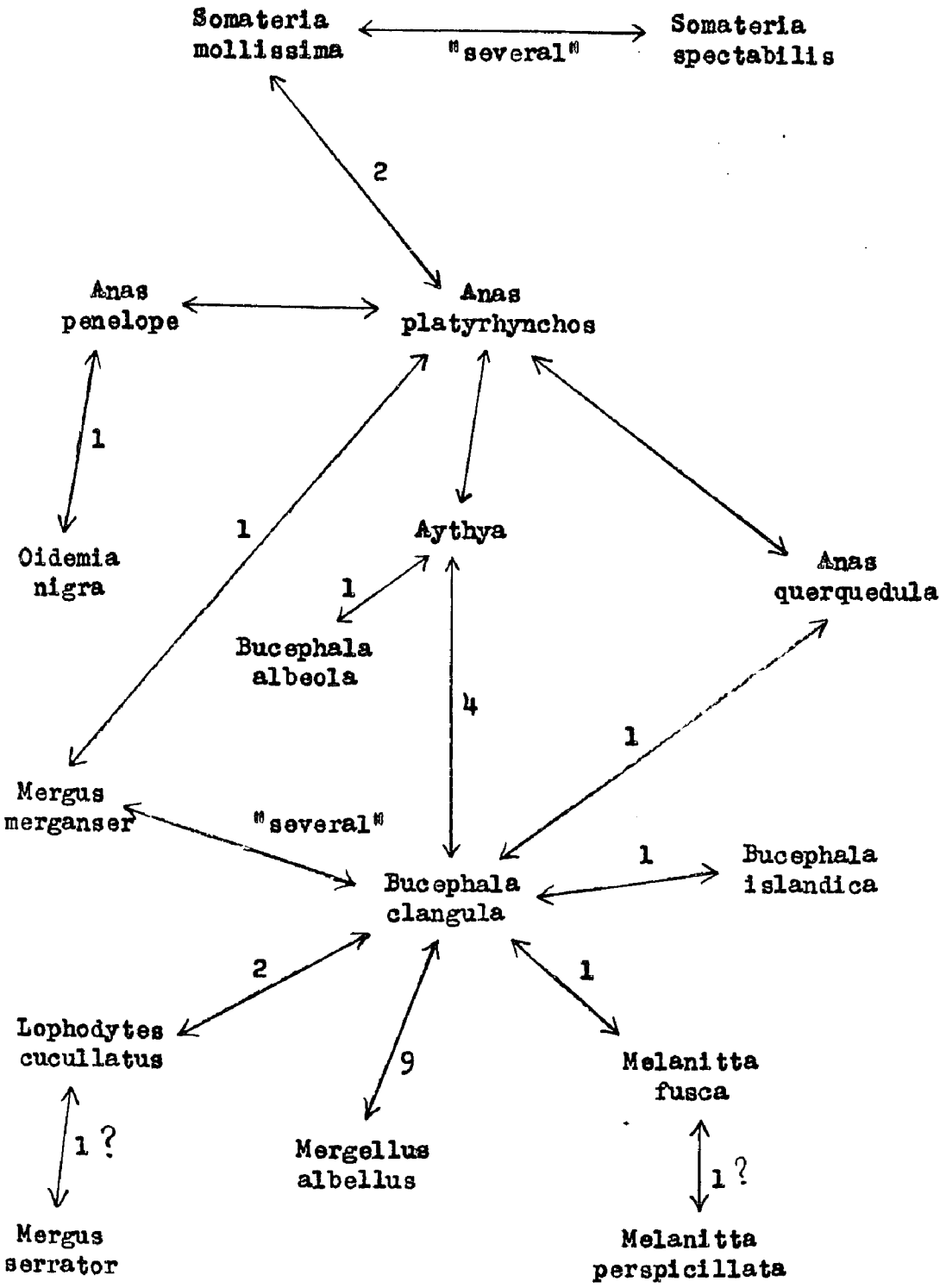


Figure 4. Hybrids involving species in the Tribe Mergini; numbers between species signify number of known hybrids.

at least four examples (not all different crosses) involving Bucephala and Aythya. There are no known hybrids between Somateria and any of the genera in the scoter - golden-eye - merganser group, but there is at least one example of a cross between Somateria and Anas (see Figure 4).

Display.-- That courtship and display characters are of great significance to the systematist has been well established by Lorenz and others. My personal observations of the display and courtship habits of Mergini are so few that I do not feel qualified to comment on their phylogenetic significance. Lorenz (1951:159) says "the task of making a purely descriptive inventory of the behavior of very many species makes very great demands on the examiner's powers of observation. In order to make, even approximately, a sufficiently complete inventory, the observer must live with the animals day after day, year after year. It is really impossible to gain the necessary knowledge by observing the animals in the wild state." It is my personal opinion (based on my own observations and a survey of the literature of the subject) that the scoters, golden-eyes, and mergansers have much in common with respect to courtship display and that the courtship of the eiders is quite different. However, before any trustworthy statement on this subject can be made a study comparable in thoroughness to Lorenz' study of the Anatini will be necessary.

Locomotor and food habits will be discussed in detail in Chapters III and IV.

D. Validity of the Tribe Mergini.

Delacour and Mayr's evidence for the validity of the Tribe Mergini can be divided into several categories based on attributes which are:

1. diagnostic of the Tribe Mergini,

2. characteristic of not only the Tribe Mergini but also members of other tribes,

3. not characteristic of all the members of the Tribe Mergini.

It is noteworthy that none of Delacour and Mayr's evidence is drawn from structural or behavioral features that could be termed diagnostic for every one of the members of the Tribe Mergini. Even a combination of all the "second category" evidence results in a definition of the Mergini which is not so well limited that members of other Tribes (Oxyurini and Aythyini) can be excluded. The best possible diagnosis of the Tribe Mergini (in terms of Delacour and Mayr's evidence) includes no structural characteristics at all; it reads as follows: members of the Tribe Mergini all have the diving habit, eat predominantly animal food, have short wings and heavy flight, and an elaborate display; most of them are brightly colored, silent birds which spend part of their time at sea, and are cold or temperate northern hemisphere in distribution.

There is more evidence favoring a separation of the golden-eyes and mergansers from the eiders than there is evidence supporting their placement together in the Tribe

Mergini. It also seems clear that the scoters and the Old-squaw should be grouped with the golden-eyes and mergansers. The Harlequin possesses a mixture of characteristics so that its possible affinities are not clear.

The morphology of the tracheas of the various species in the Tribe Mergini leads me to believe that the following forms are related: the Common Scoter (characterized by a trachea which lacks swellings and lacks a bulla), the White-winged and Surf scoters (characterized by tracheas with swellings and with type-2 bullas), and the Old-squaw, golden-eyes, and mergansers (characterized by tracheas with swellings and with type-3 bullas). A comparison of the tracheal bullas of the golden-eyes, mergansers, and Old-squaw reveals a great many structural similarities. The tracheal bullas in these three groups can be matched structure for structure. It is more difficult to compare the tracheal bullas of the scoters with those of the golden-eyes, and mergansers. However, there are some similarities among the tracheas of the Surf and White-winged scoters and those of the Old-squaw, golden-eyes, and mergansers. These similarities, perhaps unconvincing by themselves, are strongly bolstered by the occurrence of mid-tracheal swellings in both groups.

The eiders (characterized by tracheas which lack swellings and which have type 4 bullas) cannot be easily placed with the scoter - golden-eye - merganser group on the basis of the structure of the trachea and the tracheal bulla.

On the basis of the plumage patterns of adult and immature females and of downy young, Delacour and Mayr's Tribe Mergini

can be divided into two groups: 1) the eiders, and 2) the scoters, Old-squaw, golden-eyes, Harlequin, and mergansers.

The number of hybrids in the Tribe Mergini, and the different parent species involved, suggest that the scoter - golden-eye - merganser group is distinct and not related to the eider group. However, the number of recorded crosses is so low and their taxonomic significance so poorly understood that it seems unwise to depend on this evidence.

In summary, Delacour and Mayr's Tribe Mergini is a poorly defined group. The structure of the trachea and the plumage patterns of the adults and young suggest that the eiders are not related to the scoters, golden-eyes, and mergansers. On the assumption that the scoters, golden-eyes, Old-squaw, and mergansers are a monophyletic group, I am presenting a more detailed discussion of those species in the following section. I am uncertain about the affinities of Histrionicus; because of its tracheal structure I will discuss the species along with the eiders.

III. THE SCOTER - GOLDEN-EYE - MERGANSER GROUP

I have shown that the Tribe Mergini, as characterized by Delacour and Mayr, is a heterogeneous group and that the eiders (and perhaps the Harlequin) are probably not related to the rest of the genera. However, once the eiders and the Harlequin are removed from the Mergini, I am in complete agreement with Delacour and Mayr's classification of the Tribe.

In this section I shall describe various attributes of the members of the scoter - golden-eye - merganser group in an effort to shed light on their relationships with one another.

A. Plumage

The plumage patterns of the scoter - golden-eye - merganser group were studied from specimens (skins) representing all the genera and most of the species in the group. I did not examine specimens of the downy young of Melanitta perspicillata, Mergellus albellus, Mergus squamatus, Mergus australis, and Mergus octosetaceus. Downy young of all except the above-mentioned three species of Mergus are figured in the literature of the group and have been well described. I did not examine specimens of Mergus squamatus and Mergus australis in adult plumage; both species, however, are figured in Phillips (1926:298, 302) and have been thoroughly described there.

1. Downy Young

Scoters.-- Phillips (1926:5-6) gives the following description of the downy young Oidemia nigra: "dark brown to sooty black above and without any white or light-colored dorsal patches. The dark brown of the upper side extends down on the upper breast; sides and lower abdomen gradually fading into the lighter colors of the lower parts, which are light gray or in some cases almost white. The face is more or less gray, shading into an even lighter gray on the throat where it may be almost white. Usually a small white spot borders the eye on the lower side. There is no face-pattern and no clear-cut line between the shading of the upper and the lower sides."

I have examined one downy young of Oidemia nigra americana, (H. B. Conover Coll. No. 3664); Conover estimated that the bird was "about 60 hrs old." The face of this specimen has a distinct pattern, comparable to that of Melanitta fusca; the cheeks are light gray rather than white, and the demarcation between dark cap and light cheek is a sharp one. In this specimen the gray of the cheek does not grade into the dark of the cap. In all other particulars Conover's specimen and Phillips' description are in accord.

The downy young of Melanitta perspicillata is described by Phillips (1926:47) as follows: "the body coloring...is dark gray-brown above, without any spots on the wing rudiments, scapular areas or sides of rump. The coloring of the upper side merges gradually into the pale silvery gray of the abdomen.

The top of the head, down to and just below the eye, is very dark brown, almost black, rather sharply separated from the paler cheeks, throat and chin. The under side of the neck and the upper breast are gray-brown like the mantle."

Two specimens of downy young Melanitta fusca (deglandi) are dark brown above and, except for a narrow brown band across the upper breast, white below. The pattern of the head is apparently the same as that of M. perspicillata, but the contrast between dark cap and light cheek is much more marked in M. fusca, although not as striking as in Bucephala. The upper and posterior part of the cheek in M. fusca is grayish-white. Downy young of M. fusca differ from those of the other two scoters in having three (sometimes two) pairs of light markings on the upper surface of the body. The most anterior of these is the scapular spot which is white and consists of a few plumes of down located near the base of the wing. The scapular spot in one specimen (UMMZ 121,344) is so inconspicuous as to be easily overlooked; the few white plumes are obscured by plumes of dark down. Posteriorly there is a pair of inconspicuous white rump spots, one on either side of the rump at the base of the tail (absent in UMMZ 121,344). Over the proximal part of the leg there is a narrow femoral band of grayish-white, oriented along a dorso-ventral line, and continuing uninterrupted into the white of the belly. The dorsal wing surface is dark except for a faint ulnar band of grayish-white running along the posterior margin of the wing in the ulnar region. The under surface of the wing is dark except for a white patch on the

proximal part of the manus. There is a large patch of white down in the axillar area.

Clangula.-- Downy young of Clangula hyemalis are dark brown above and, except for a narrow brown band across the upper breast, white below. The pattern of the head is similar to that of downy Melanitta fusca; the dark cap extends well below the eye and contrasts sharply with the cheeks and ventral part of the head, which are white. There are three small light marks around the eye; these vary in shape and extent. There may or may not be a small light spot in the lore. The upper surface of the body and wings is uniformly dark brown, unrelieved by white scapular, rump, or ulnar markings. The underside of the wing is white except for a brown spot on the proximal end of the manus and a brown patch covering most of the patagium and radius and ulna. There is a small patch of white down in the axilla.

Bucephala.-- The downy young of the three species of Bucephala are so similar that they do not warrant separate descriptions here.

Downy young of Bucephala are dark brown above with three pairs of white markings; the lower parts are white except for a narrow brown band across the upper breast. A dark cap covers the entire top of the head, center of the nape, lores, and malar area and extends down the sides of the head well below the eye. The dark of the cap is in sharp contrast to the white ventral coloring of the head, which covers the chin, neck (down to the dark band across the upper breast) and the

cheeks. The paired white dorsal markings are prominent in Bucephala and consist of a scapular spot (at the base of the wing), a rump spot (side of rump at base of tail), and a narrow femoral band. The dorsal surface of each wing is dark except for a narrow ulnar band of white. The down covering the ventral surface of each wing is short and white except for a small brown patch at the wrist (B. islandica). B. clangula and B. albeola differ from B. islandica in having a brown patch over the proximal part of the radius and the distal part of the humerus. The trailing edge of the manus has long, dark plumes of down. There is a small patch of white down in the axillar area.

Mergellus.-- Dresser (1874:670) describes the downy young Mergellus as follows: "upper parts, including the sides of the head below the eye, but only the back of the neck, dark blackish brown, darkest on the crown and the lower part of the back; at the base of the wing joint a white spot, and another close to it, but rather lower down the back, and on either side of the rump another white spot; below the eye a very small white spot; under parts white; breast and flanks pale grayish or sooty brown."

Phillips (1926:231) says "according to Salvadori (1895) the upper parts, including the sides of the head below the eye, but only the back of the neck, are dark brown. Below the eye a very small white spot and white spots on the posterior edge of the wing, the sides of the rump, and on the flanks. The throat and sides of the upper part of the neck

conspicuously white; crop region dusky; flanks brown; breast and abdomen white."

From the above descriptions the downy young Mergellus must closely resemble downy young of Bucephala, perhaps the only difference being that the latter lack the white spot below the eye. Dresser (1874: plate no. 454) figures the downy young of Mergellus albellus; from the figure, downy Mergellus is indistinguishable from downy Bucephala.

Lophodytes.-- Downy young Lophodytes is dark brown above with three pairs of white markings; the lower parts are white except for the upper breast which is grayish, and the face and throat which are rufous. A dark cap covers the entire top of the head, center of the nape, and the lores, and extends down the sides of the head to the ventral margin of the eye. The dark cap contrasts with the light rufous ventral coloring of the head, which covers the chin, cheeks, and throat. Posteriorly the rufous throat coloring changes to pale gray at the upper breast. The paired white dorsal markings are smaller than in Bucephala. They consist of a scapular spot, a rump spot, and a narrow femoral band. The dorsal surface of each wing is dark except for a narrow ulnar band of white. The under surface of the wing is white except for a brown spot on the base of the manus. The ventral side of the alula is brown. The white wing lining extends over the leading edge of the wing so that in dorsal view the wing appears to be bordered anteriorly with white. There is a patch of white down in the axillar region.

Mergus.-- The following description treats Mergus merganser (americanus) and Mergus serrator; the downy young of Mergus squamatus and Mergus octosetaceus have never been described. I will treat downy Mergus australis separately below.

Downy Mergus merganser and M. serrator have dark brown upper parts and white underparts which lack a dark band across the upper breast. The crown, nape, and sides of neck are dark brown, forming a dark cap which extends below the eye; its lower margin is a dark streak from the base of the bill above the lore through the eye. A narrow white patch extends from below the eye anterior to include the lore. A dark malar streak, beginning at the base of the upper mandible, extends posteriorly, forming the lower limit of the subocular patch of white. The dark malar streak fades out posteriorly, merging into a reddish-brown "wash" which covers the sides of the face (posterior to the eye) and neck below the dark upper markings; this "wash" extends ventrally at the lower neck and becomes fainter. The chin, throat, and sides of the face up to the malar stripe (and more posteriorly up to the pale reddish-brown area on the face and sides of the neck) are white. The paired white dorsal body markings consist of a small white scapular spot, a large white rump spot, and a broad white femoral band. The dorsal surface of the wing is brown except for a narrow ulnar band of white. The underside of the wing is unmarked white in Mergus serrator, and white with a brown wrist-patch (of varying size) in Mergus

merganser. In both species the white wing lining extends over the leading edge of the wing so that in dorsal view the wing appears to be bordered anteriorly with white. There is a patch of white down in the axillar region.

Phillips (1926:299) describes downy young Mergus australis as follows: "compared with the young of the Red-breasted Merganser this species is very much darker, almost coal black above, and there is only the faintest trace of light-colored wing-, scapular- and rump-patches. The chin, throat and upper breast are rusty red, not white as in Mergus serrator, while the remainder of the lower side is light gray instead of pure white."

2. Adult Plumage Characters

It is not my purpose in this section to present detailed descriptions of the plumages of each of the species in the scoter - golden-eye - merganser group. Rather, I shall describe in a general fashion some of the pattern characteristics which may help clarify the relationships within the group. The following generalizations may be made:

1. From the scoters to the Old-squaw, golden-eyes, and mergansers there is a reduction in the amount of black in the plumage of the adult male.

2. The dark cap pattern characteristic of the downy young of most of the species reappears or is suggested in the female and/or immature plumages of some of the species. (Oidemia, Melanitta, Bucephala albeola, Mergellus).

3. The head plumage of the adult male is predominantly black (iridescent dark colors in Bucephala) in all species except Mergellus albellus and Mergus australis.

4. Except for three species (Oidemia nigra, Melanitta perspicillata, and Clangula hyemalis) both sexes have extensive white on the proximal part of the wing (dorsal surface). This white area always includes most of the secondaries; it may also include most of the greater upper secondary coverts and, in some species, a varying number of the lesser upper secondary coverts. The white proximal wing patch is found in both sexes and is generally less extensive in females than in males.

5. All members of the group except the scoters have elongate head feathers. These are poorly developed in male Clangula, well developed in males of Bucephala but not females. The head feathers of male (but not female) Mergellus are so elongate that they can be termed a crest. Males and females of Lophodytes and four of the five species of Mergus have well developed crests. The male of Mergus merganser has short plumage on the head; the female is crested.

6. Female and juvenile plumages in the group are either predominantly dark brown or gray. Juveniles of all species and females of most have lighter underparts than upper parts. The heads of the female and juvenile scoters and Buffle-head do not contrast with the rest of the upper parts; those of the golden-eyes and the mergansers are reddish-brown and contrast with the gray upper parts.



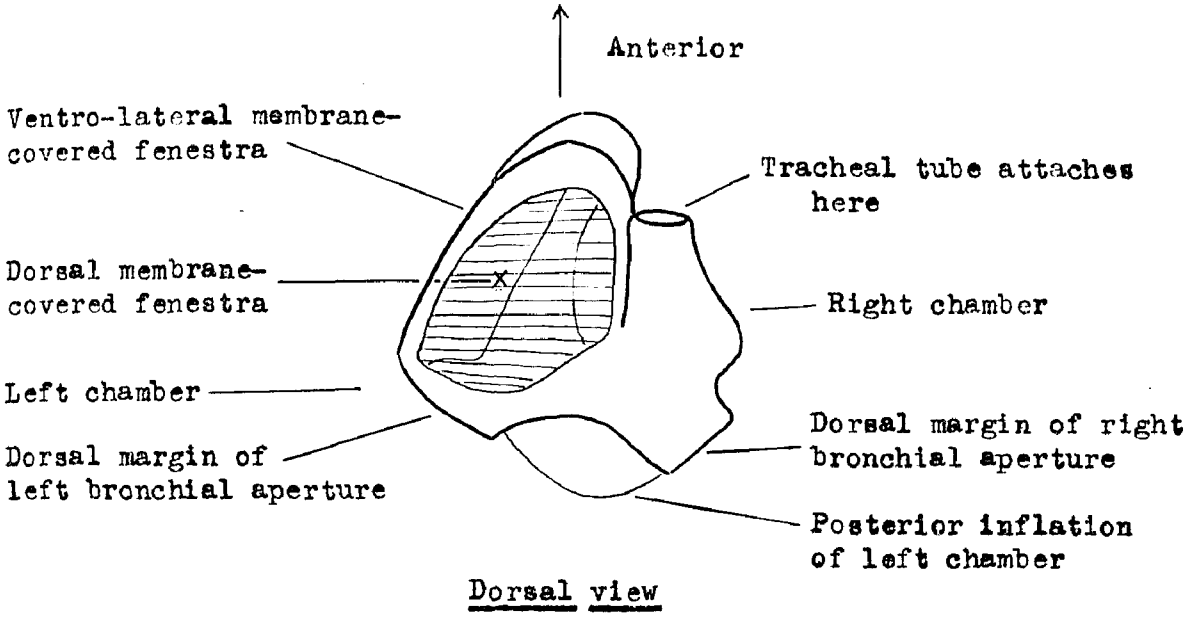
B. Trachea

I have examined specimens of the tracheal bulla of all the species in the scoter - golden-eye - merganser group. Complete tracheas (in most cases preserved in fluid) were examined for all species in the group except Mergus octosetaceus and Mergus squamatus.

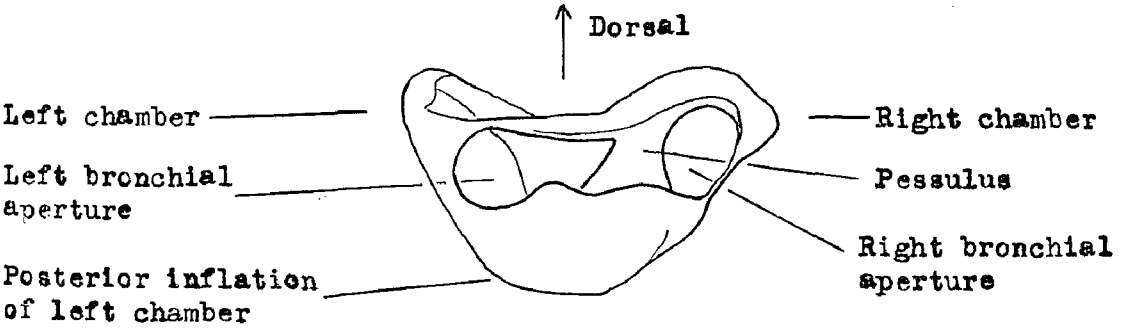
1. Tracheal Bulla

The tracheal bulla is at the lower (posterior) end of the trachea; it opens anteriorly into the tracheal tube and posteriorly into the right and left bronchi. The tracheal bulla consists of a right and left chamber separated medially by a vertical septum, the pessulus. Each of the chambers of the tracheal bulla opens into the bronchus on its side. The tracheal bulla in the scoter - golden-eye - merganser group is in part osseous and in part membranous. Among the different species the two chambers vary in size, amount of bony structure, and amount of membrane. The two chambers also vary interspecifically in degree of ossification and consequently in amount of visible ring-structure. The extent of ossification varies intraspecifically with age. As far as I can tell this only affects the number of partially fused rings; age variations do not seem to affect the size or number of membrane-covered fenestrae once the bulla has attained adult size.

Scoters.-- The tracheal bulla is absent in Oidemia; instead, the males have (in common with the females) a small, partially fused, bilaterally symmetrical structure. In



Dorsal view



Posterior view

Figure 6. Structure of the tracheal bulla of Mergus merganser.

posterior view, the right and left posterior (or bronchial) apertures are very similar in size and shape. The pessulus appears as a delicate, dorso-ventral bar separating the right and left chambers.

The tracheal bulla of Melanitta is also bilaterally symmetrical (or almost so). However, it differs from that of Oidemia in the following respects:

1. The left chamber extends a little farther laterally than the right.

2. Both chambers are slightly inflated.

3. The antero-posterior length of the bulla is greater; i.e., the bulla is composed of more tracheal rings.

4. A membrane-covered opening is present on the ventro-lateral surface of each chamber near the posterior margin.

5. There is a dorso-lateral protrusion (antero-posterior oriented ridge or fold) on each chamber.

6. There is a lateral, membrane-covered fenestra on each side of the bulla near its anterior margin.

7. The pessulus in posterior view appears as a very narrow, delicate bar; in lateral view, however, it is much wider (antero-posteriorly) than that of Oidemia.

Old-squaw.-- The right chamber of the tracheal bulla of Clangula is only slightly inflated; it is, however, well ossified. The left chamber is much inflated dorso-laterally; it is also inflated in a posterior direction close to the midline. The left chamber has a large, membrane-covered

Figure 6. Tracheal bullas of species in the scoter - golden-eye - merganser group.

a. Oidemia nigra

b. Melanitta fusca

c. Clangula hyemalis

d. Bucephala albeola

e. Bucephala clangula

f. Mergellus albellus

g. Lophodytes cucullatus

h. Mergus serrator

i. Mergus octosetaceus

j. Mergus merganser

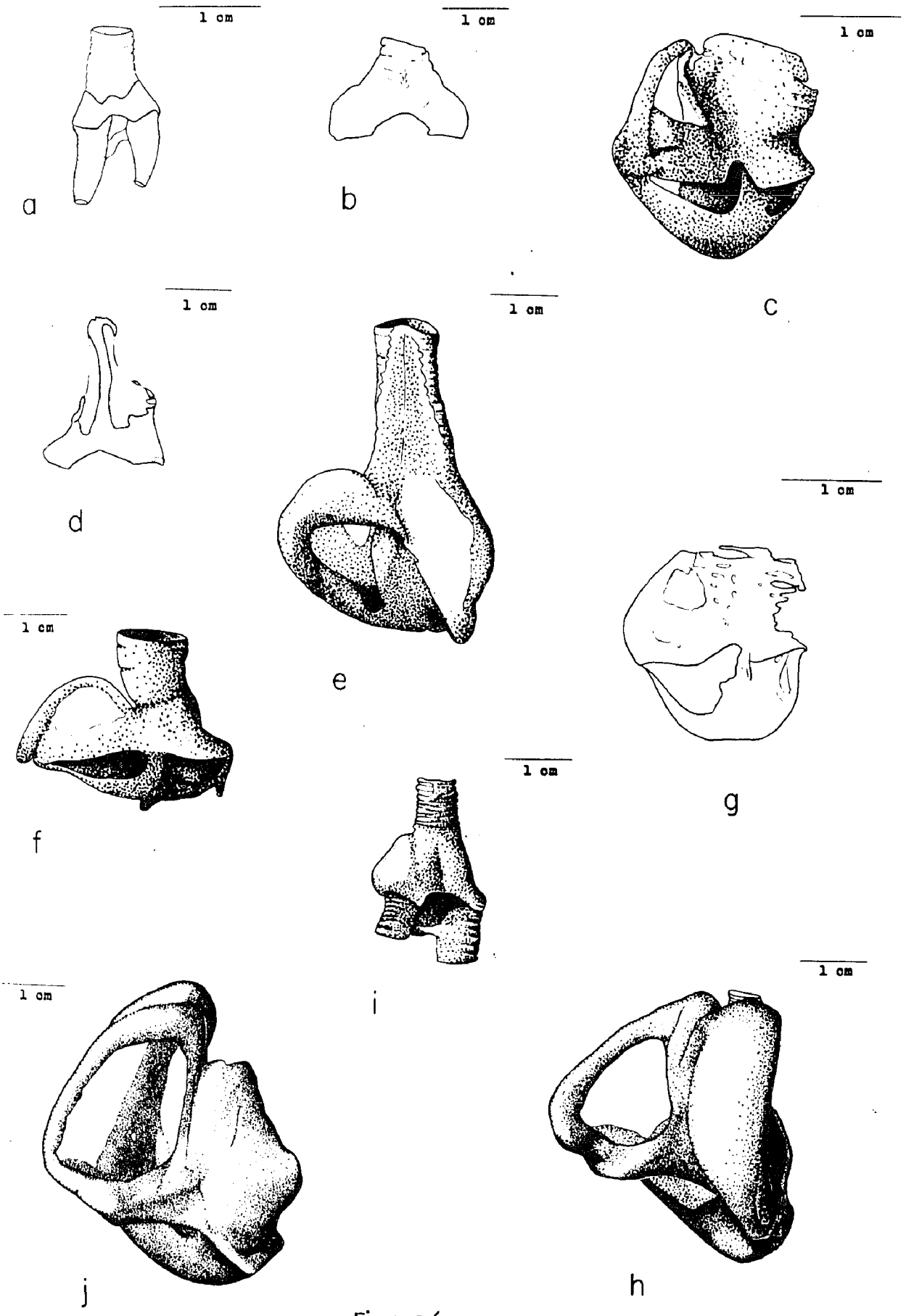


Figure 6.

fenestra on its dorso-medial surface. The anterior margin of the left chamber consists of a thin, bony bar which supports the anterior margins of both membranes. This bar is in the form of an arch and extends, from a position near the left wall of the trachea, dorsally and then posteriorly to lap over the posterior wall of the left chamber near the dorsal-most margin of the left bronchial aperature. The left chamber appears to have grown up around the posterior extension of the tracheal tube (now fused to form the anterior part of the tracheal bulla) and is separated from it by a heavy fold of bone. The posterior inflation of the left chamber has a bulbous appearance and extends farther caudad than the dorsal margins of the bronchial apertures; there is at the midline a ventral inflation which continues caudad into the posterior inflation. In posterior view the pessulus appears stouter than in Melanitta and is much thicker (laterally) in its ventral part. In lateral view, the pessulus is very wide antero-posteriorly. The five tracheal rings anterior to the tracheal bulla are highly modified so that on the ventral side of the tracheal tube there are five membrane-covered fenestrae.

Buffle-head.-- Both chambers of the tracheal bulla of Bucephala albeola are inflated; the right chamber is slightly larger than the left. In posterior view the left chamber is slightly inclined dorsad. Both chambers are mostly membrane-covered; the supporting bony structure is very thin and fragile and shows indications of its origin from tracheal rings. The

pessulus in its posterior aspect is thin; in lateral view it is narrow (antero-posteriorly) at its dorsal end and becomes very wide at its ventral inflation in the midline of the posterior end of the tracheal bulla at the ventral end of the pessulus.

Golden-eyes.-- The tracheal bullas of the two golden-eyes are so similar that they do not warrant separate descriptions. Both chambers are inflated, the left one much more than the right. The left chamber is much inflated dorso-laterally; in posterior view the long axis of the bronchial aperture runs from ventro-medial to dorso-lateral. The left chamber is in large part membrane-covered. The membrane is attached along its posterior margin to the broad, bony base of the left chamber; anteriorly, the membrane is attached to the wall of the fused continuation of the tracheal tube. The tracheal bulla is very long (5.5 cm.); the anterior third of its length is roughly tubular, divided internally by an anterior continuation of the pessulus, and composed of rings which are fused together along their dorsal and their ventral margins. The right and left walls of the anterior tubular part of the tracheal bulla are in part membrane-covered. The amount of membrane in the left wall is less in more mature specimens. The left chamber has a large ventral inflation posteriorly and medially. The right chamber is roughly flask-shaped in lateral view. Much of its lateral wall is poorly ossified and the basic ring-structure can be discerned. The dorsal surface of the right chamber has a

large membrane-covered fenestra. The pessulus in posterior view appears to be very thick. Actually, it is a thin sheet of bone which forms the medial wall of the right chamber; it bulges to the left considerably, which gives it the appearance of thickness. Anteriorly the pessulus becomes complex, giving rise to several bony folds, some of which join the right inner wall of the right chamber. The pessulus also gives rise to a long process of bone which extends anteriorly, forming a dorso-ventral septum partially dividing the inside of the anterior tubular part of the bulla. The inner dorsal and ventral surfaces of the anterior tubular part of the bulla each has a bony fold corresponding to the dorsal and ventral margins of the anterior process of the pessulus.

Smew.-- Both chambers of the tracheal bulla of Mergellus are inflated, the left one considerably and the right one only slightly. The left chamber is inflated mostly laterally but also slightly dorsally. Its dorsal and ventro-lateral walls meet anteriorly to form an edge which extends from medial and ventral to lateral and slightly dorsal. A large, membrane-covered fenestra occupies most of the dorsal wall. The anterior part of the ventro-lateral wall of the left chamber has a large, membrane-covered fenestra. The anterior margins of the membranes of both fenestrae are supported by the slender bony arch which forms the anterior edge of the left chamber. A bony process from the posterior margin of the ventro-lateral fenestra partially divides the fenestra. If this process were extended anteriorly to the bony arch



which forms the anterior edge of the left chamber, the trifenestrate condition of Mergus merganser would result.

The right chamber is only slightly inflated but is well ossified. It lacks a membrane-covered fenestra.

The ventro-medial wall of the left chamber is inflated ventrally and extends slightly posteriorly. The ventral and posterior part of the pessulus is broadened and bulges posteriorly; anteriorly, the ventral margin of the pessulus is deflected to the right where it is attached to the ventral wall of the bulla. A medial continuation of the ventral expansion of the left chamber underlies the pessulus, which is attached along its dorsal margin to the midline of the dorsal wall of the bulla. It extends ventrally and to the left on a slant. The tracheal bulla of Mergellus is quite unlike that of Lophodytes.

Hooded merganser.-- Both chambers of the tracheal bulla of Lophodytes are inflated, the left chamber much more than the right. The left chamber is inflated laterally; its dorsal wall and its ventro-lateral wall meet dorso-laterally to form an edge or fold which runs from anterior and ventro-medial to posterior and dorso-lateral. The dorsal wall of the left chamber has an irregularly shaped membrane-covered fenestra in its anterior part; the ventral wall also has a membrane-covered fenestra in its anterior part. The left chamber has a large inflation which extends posteriorly on the medial-ventral side of the tracheal bulla. This posterior inflation is bulbous in appearance and extends far posterior to the

dorsal margin of the bronchial apertures. The right chamber is slightly inflated (much more than in M. octosetaceus) and very little ossified. In its anterior part it is formed of rings which are fused ventrally to the median ventral part of the bulla and dorsally to the median dorsal part of the bulla. Posterior to the rings there is a large membrane-covered fenestra which occupies most of the wall of the right chamber. The pessulus in posterior view forms a thin vertical septum between the right and left chambers. The posterior inflation of the right chamber in part underlies the ventral attachment of the pessulus. In lateral view the pessulus is very wide antero-posteriorly; it is attached ventrally along the midline of the ventral wall of the bulla. Dorsally the pessulus is attached to the midline of the dorsal wall of the bulla.

Brazilian merganser.-- Both chambers of the tracheal bulla of Mergus octosetaceus are inflated, the left one much more than the right. The left chamber is inflated laterally and slightly dorsally; its dorsal wall and its ventro-lateral wall meet dorso-laterally to form an edge which extends from anterior and ventro-medial to posterior and dorso-lateral. The dorsal wall of the left chamber is almost completely occupied by a large, membrane-covered fenestra. The anterior part of the ventro-lateral wall of the left chamber is also almost completely occupied by a large, membrane-covered fenestra. The left chamber has a large inflation which extends posteriorly on the medial, ventral side of the tracheal

bulla. This posterior inflation is bulbous in appearance and extends far posterior to the dorsal margins of the bronchial apertures. The left chamber of the tracheal bulla of Mergus octosetaceus is very similar to that of Lophodytes; the only differences are:

1. The left chamber in Lophodytes is more inflated but has the same shape.

2. The two membrane-covered fenestrae are larger (relative to chamber size) in Mergus octosetaceus.

3. The posterior, ventral inflation is smaller in Mergus octosetaceus and does not in its more anterior medial part underly the pessulus to form a slight (longitudinal) bulge in the ventral medial wall of the tracheal bulla.

The right chamber of the tracheal bulla of Mergus octosetaceus is well ossified, only slightly inflated, and shows little indication of the basic ring structure. The right chamber lacks a membrane-covered fenestra. I was unable to examine the pessulus of Mergus octosetaceus.

Red-breasted merganser.-- Both the right and left chambers of the tracheal bulla of Mergus serrator are very much enlarged. The left chamber is inclined dorso-laterally; its dorsal wall contains a large membrane-covered fenestra. Its ventro-lateral wall also contains a large membrane-covered fenestra. The dorsal and ventro-lateral walls of the left chamber meet dorso-laterally to form a fold or edge which extends from anterior and ventro-medial to posterior and dorso-lateral. On comparing left chambers of Mergus

serrator and Lophodytes it can be seen that the orientation and relations of the two are very similar. The principal differences between the two are in amount of ossification (much more in M. serrator), amount of inflation (much more in M. serrator), and extent of the two membrane-covered fenestrae (both much larger in M. serrator). The left chamber has a large, bulbous inflation which extends posteriorly from the median ventral portion of the tracheal bulla. Anterior to the posterior inflation, a part of the left chamber underlying the pessulus has become inflated and forms a longitudinal bulge in the ventral medial wall of the tracheal bulla; a similar condition (less well developed) exists in the tracheal bulla of Lophodytes. The right chamber of the tracheal bulla of Mergus serrator is inflated as much as the left one. The right chamber is inflated dorsad; its plane is roughly at right angles to the plane of the left chamber. A large, membrane-covered fenestra forms most of the lateral wall of the right chamber. The pessulus is a thick vertical plate of bone separating the right and left chambers. Fused dorsally and ventrally to the walls of the tracheal bulla, the pessulus extends almost to the anterior end of the bulla; it stops just posterior to the entrance of the tracheal tube. The pessulus of Lophodytes is very similar in all respects to that of Mergus serrator.

Goosander, Chinese merganser, Auckland Island merganser.--The tracheal bullas of Mergus australis, Mergus squamatus, and Mergus merganser are very similar; the following description

applies to the bullas of all three species. Both chambers of the tracheal bulla are inflated, the left one much more so than the right. The right chamber is much more inflated than in Mergellus. Compared to that of Mergellus, the tracheal bullas of these three species are very long (antero-posteriorly). The left chamber is inflated laterally; its anterior extremity extends much farther cephalad than in Mergellus. The left chamber anterior to the left bronchial aperture has three walls, the dorsal wall in merganser and australis has a large membrane-covered fenestra occupying most of the wall; this fenestra is smaller in squamatus. The dorsal wall and the ventro-lateral wall meet laterally and slightly dorsally, forming an edge which extends from anterior and medial to posterior and lateral. The ventro-lateral wall of merganser has a large membrane-covered fenestra; in squamatus this fenestra is smaller, The ventro-lateral and ventro-medial walls meet ventrally to form an edge which extends from anterior to posterior. The ventro-medial wall of merganser bears a large membrane-covered fenestra; this fenestra is much smaller in squamatus. The anterior extent of the left chamber is greatest in merganser and least in squamatus and australis. Mergus merganser and australis are the most similar in general conformation of the anterior part of the left chamber. The ventral and posterior part of the left chamber is inflated posteriorly. This inflation is very large in squamatus, smaller in merganser, and smallest in australis. The right chamber is largest in squamatus and smallest in merganser; that of australis is between the

extremes. This chamber bulges dorsally and has a lateral inflation which bulges to the right. The pessulus forms a vertical septum separating the right and left chambers. In merganser the pessulus extends anterior only two-thirds the distance to the tracheal aperture; the pessulus extends farther anterior in squamatus and terminates close to the tracheal aperture.

2. Tracheal Tube and Bronchi

The trachea of ducks is a long tube -- not always of uniform diameter -- composed of cartilaginous or bony tracheal rings. The tube of the trachea begins anteriorly at the larynx and ends posteriorly in a fused, partly bony and partly cartilaginous structure at the posterior end of which the two bronchi arise. The bronchi consist of cartilaginous rings or semirings. The following discussion treats variations in the structure of the trachea and bronchi in males of the scoter - golden-eye - merganser group.

Scoters.-- The tracheal tube of male Oidemia nigra americana is of uniform diameter for most of its length; in the posterior-most quarter of its length the diameter of the tube tapers to about half its anterior diameter. The tracheal rings are formed mostly of cartilage; they become slightly wider at the posterior end of the trachea. Both bronchi are enlarged and increase in diameter posteriorly; prior to entering the lungs they become much reduced in diameter.

Figure 7. Tracheas of species in the scoter - golden-eye - merganser group: scoters, Old-squaw, and golden-eye.

a. Oidemia nigra

b. Melanitta perspicillata

c. Melanitta perspicillata

d. Melanitta fusca deglandi

e. Melanitta fusca fusca

f. Clangula hyemalis

g. Bucephala albeola

h. Bucephala clangula

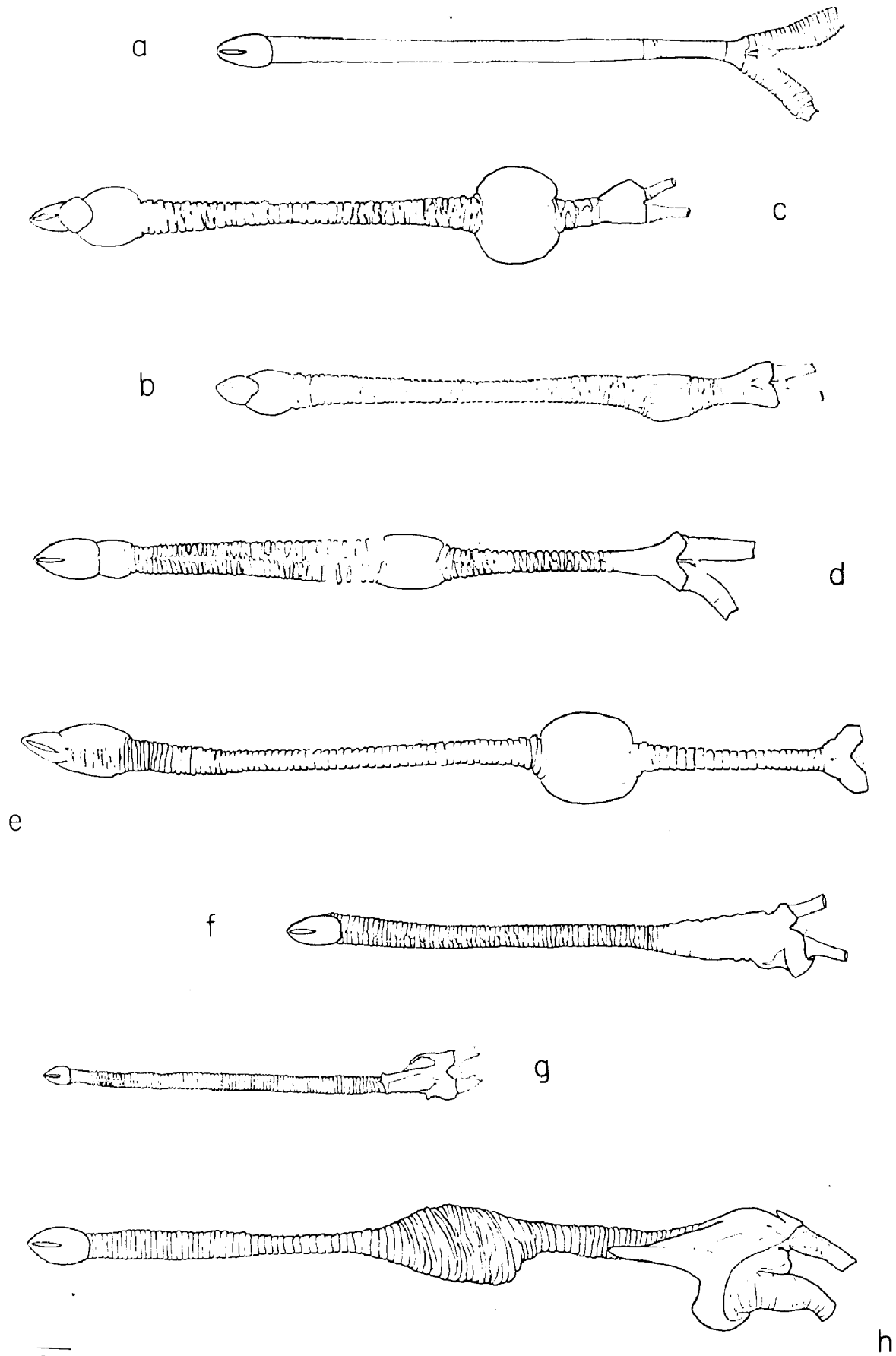


Figure 7.

The tracheal tube of male Melanitta perspicillata has a dilation at its anterior end, just behind the larynx, and another dilation at its posterior end close to the tracheal bulla. Both dilations show considerable variation in size and shape. The anterior dilation is a hollow, bony expansion composed of fused tracheal rings. A frontal section through the anterior dilation reveals that it is a simple expansion of the wall of the trachea. Ventrally, on the interior of the dilation, there are two chambers separated medially by a wide, antero-posteriorly oriented ridge. The anterior dilation may be either partly or completely ossified; the larger the dilation the more completely ossified it is. The trachea tapers to its smallest diameter midway between the anterior and posterior dilations, and then gradually increases in diameter towards the posterior dilation. The posterior dilation is formed of fused tracheal rings. In three different individuals it varies in width from slightly wider than the tube of the trachea to about three times as wide. The dilation is mostly lateral; in its dorso-ventral dimension it attains a width only slightly greater than that of the trachea. At its largest, the posterior dilation appears roughly circular in ventral view and is completely ossified. When small, the posterior dilation is little more than an oblong swelling in the trachea; although the rings are fused together, their outlines can be discerned. The tracheal rings throughout the length of the trachea are entirely bony. The bronchi are of equal size and are not enlarged.

The tracheal tube of male Melanitta fusca has two enlargements, one just posterior to the larynx and one about two-thirds the distance from the larynx to the tracheal bulla. I have examined several tracheas of Melanitta fusca deglandi and one trachea of Melanitta fusca fusca; I saw no evidence of variation in the structure of the trachea of deglandi. The tracheas of both subspecies have an anterior dilation which is similar in external appearance to that of Melanitta perspicillata. Internally, the anterior dilation of Melanitta fusca deglandi consists of two ventral chambers separated from one another by a median ventral bony septum, and separated from the main tube of the trachea by a bony wall. At the posterior end of the two chambers there is a pair of circular openings which connect the right and left chambers to the main tube of the trachea. The anterior dilation is larger in Melanitta fusca fusca than in Melanitta fusca deglandi. I have not examined the internal structure of the anterior tracheal dilation of Melanitta fusca fusca and am not certain that it is identical with that of Melanitta fusca deglandi.

The mid-tracheal swelling of Melanitta fusca deglandi is a bony enlargement consisting of fused tracheal rings; in ventral view it is roughly rectangular in shape. From the anterior dilation to the mid-tracheal dilation the trachea gradually increases in width to double its anterior diameter. Posterior to the mid-tracheal dilation the trachea becomes very narrow (one-third of its greatest diameter) and is uniform in width to its posterior end.



The mid-tracheal swelling of Melanitta fusca fusca appears roughly circular in its ventral aspect. Dorso-ventrally it has about the same thickness as the tracheal tube; laterally, it is about three times the width of the trachea. The tracheal tube between the anterior and mid-tracheal dilations and between the mid-tracheal dilation and the tracheal bulla is of uniform diameter. The bronchi are not enlarged.

Old-squaw.-- The trachea of male Clangula hyemalis has a single, bony swelling at its posterior end. The lower end of this dilation is fused to the tracheal bulla. The dilation consists of five highly modified tracheal rings. On the dorsal and lateral sides of the trachea the five rings are very broad; on the ventral side of the trachea each of the five rings abruptly becomes very narrow and forms a delicate, transverse bar. Between any two of these bony, transverse bars there is a membrane-covered space; there are in all five such membrane-covered spaces. From the anterior end of the tracheal swelling the trachea tapers slightly and then proceeds anteriorly maintaining a uniform diameter; the anterior-most quarter of its length is slightly wider. The tracheal rings are ossified. The bronchi are of equal size and only slightly larger than in the female.

Golden-eyes.-- The trachea of male Bucephala albeola lacks any dilations. At its laryngeal end the trachea is slightly smaller in diameter than the rest of the tube. The diameter of the tube increases gradually for a short distance

posteriorly and for most of its length is of uniform diameter. Except for the most anterior and most posterior tracheal rings which are in part or entirely cartilaginous, the trachea is composed of bony rings. The bronchi are of equal size and not at all enlarged; in contrast to the condition in the scoters and Old-squaw, the bronchi are widely separated.

The trachea of male Bucephala clangula americana has a mid-tracheal swelling a little more than half way down the trachea from the larynx. This swelling is, at its maximum, four times the smallest diameter of the trachea and it occupies about one-fifth the length of the trachea. It is composed of narrow, bony tracheal rings which vary from small to large in diameter. None of the rings is fused to any other rings; they are joined to one another by membrane. By pulling on the tracheal tube it is possible to greatly lengthen the mid-tracheal swelling. The tracheal tube at the posterior end of the swelling is about twice the diameter of the tube at the anterior end of the swelling. The trachea between the mid-tracheal swelling and the bulla is of large but uniform diameter. Anteriorly, the trachea gradually increases in diameter towards the larynx. Most of the rings anterior to the mid-tracheal swelling are cartilaginous. Posterior to the swelling each of the rings is part bone and part cartilage. The left bronchus is about twice the diameter of the right one. The bronchi are widely separated from one another.

The trachea of male Bucephala islandica has a mid-tracheal swelling which is about three times the minimum diameter of

the rest of the trachea; the swelling occupies about two-fifths of the total length of the trachea. The swelling commences just anterior to a point midway between the larynx and the tracheal bulla; it proceeds posteriorly, diminishing slightly in diameter, to terminate a short distance anterior to the tracheal bulla. The part of the tracheal tube anterior to the swelling is of uniform diameter and about half the diameter of the part between the swelling and the tracheal bulla. All the rings seem to be in part cartilage. The bronchi are of equal size, only slightly enlarged, and widely separated from one another.

Mergansers.-- The anterior third of the trachea of Mergellus albellus is of uniform diameter and about half the maximum diameter which the trachea attains more posteriorly. The middle third of the trachea gradually widens; the posterior-most half of the trachea is uniformly wide until it enters the tracheal bulla, at which point there is an abrupt constriction of the tracheal tube. The tracheal rings of the anterior third of the trachea are bony; those of the posterior two-thirds of the trachea are bony except for the dorsal surface, which is cartilaginous. Neither of the bronchi is enlarged and they are widely separated from one another.

The trachea of Lophodytes cucullatus has a dilation in its posterior-most third. From the anterior of the dilation to a point a little posterior to the larynx the trachea is of uniform diameter; it gradually increases in diameter until it joins the larynx. The dilation of the trachea is, at its maximum, twice as wide as the tracheal tube; dorso-ventrally

Figure 8. Tracheas of species in the scoter - golden-eye - merganser group: mergansers.

a. Mergellus albellus

b. Lophodytes cucullatus

c. Mergus australis

d. Mergus merganser

e. Mergus serrator

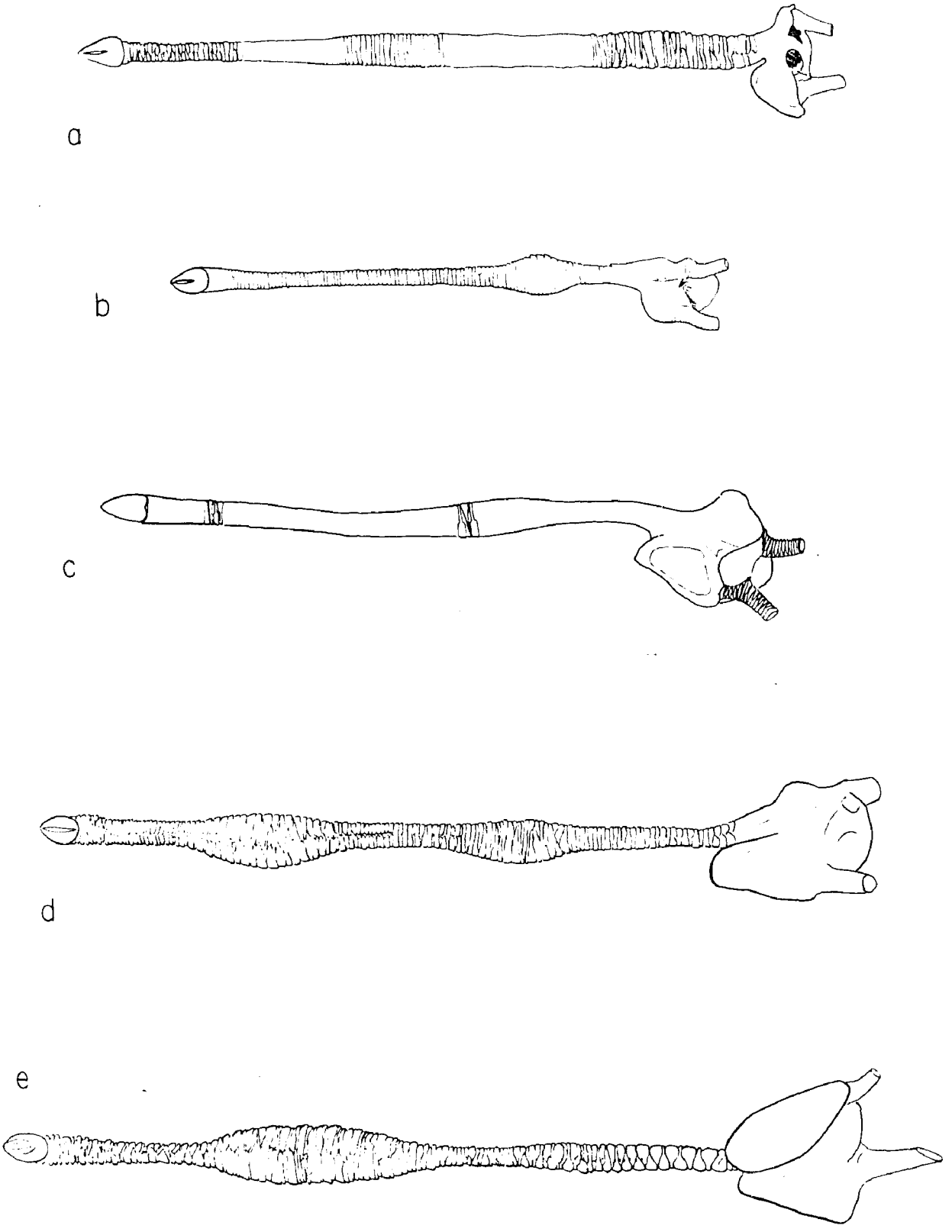


Figure 8.

it is thinner than the tracheal tube. The rings forming the dilation are not fused to one another; they are osseous ventrally and largely cartilaginous dorsally. A short length of tube, consisting of nine or ten highly modified tracheal rings, connects the dilation to the tracheal bulla. In dorsal aspect each of the posterior-most tracheal rings appears as a narrow band of bone bounded anteriorly and posteriorly by a broad membrane. Ventrally, each of the rings tapers to less than half its dorsal width. On its ventral side this part of the trachea is not round; instead, it consists of two ventro-lateral walls which meet in the ventral midline to form an antero-posteriorly oriented crest. The tracheal rings support the broad membranes of the trachea between them and form the skeleton of the antero-posteriorly oriented crest. The most anterior tracheal rings (those just behind the larynx) are in part cartilaginous; all the rest of the rings (except those in the dilation) are entirely bony. The bronchi are not enlarged, are equal in size, and widely separated from one another.

The trachea of Mergus serrator has a large swelling which begins about a quarter the distance from the larynx to the tracheal bulla and ends about half the distance to the bulla. In width this swelling is three times the diameter of the rest of the trachea; in thickness (dorso-ventrally) it is twice the diameter of the trachea. The swelling is composed of completely bony tracheal rings which are not fused to one another. Anterior to the swelling the trachea

is narrow, gradually widening towards the larynx. Posterior to the swelling the trachea has its narrowest diameter; from that point it gradually increases in width; during the last quarter of its length the trachea maintains a uniform diameter. The posterior-most twenty rings of the trachea are very narrow ventrally and are separated from one another by wide membranes. All of the rings composing the trachea are bony. The left bronchus is almost twice the size of the right one; the two bronchi are widely separated from one another.

The trachea of Mergus merganser americanus has two dilations, a large one in the anterior half of the trachea and a smaller one in the posterior half. The anterior swelling is twice as wide as the trachea and about half again as thick; it is a simple enlargement of the trachea which becomes narrower in a smooth taper anteriorly and posteriorly. The posterior dilation is similar to the anterior one but smaller. The anterior part of the trachea -- between the anterior dilation and the larynx -- is of uniform diameter. The short length of trachea joining the anterior and posterior dilations is also of uniform diameter. Below the posterior swelling the trachea gradually decreases in diameter until it joins the tracheal bulla. All of the tracheal rings are entirely bony and none show any special modifications. The bronchi are of equal size and widely separated from one another.

The trachea of Mergus australis has a single slight swelling in its posterior half. This swelling is at most one and a half times the diameter of the trachea; it is a

a simple expansion of the trachea and tapers gradually anteriorly and posteriorly until it is the same width as the rest of the trachea. Apart from the dilation, the trachea is of uniform diameter throughout its length. All of the tracheal rings are bony. The two bronchi are of equal size and widely separated from one another.

C. Ecology and Diving Habits

1. Nests and Nesting Habitats

The scoters are entirely inland and fresh water in their nesting distribution. Nests are built on the ground and very often in the shelter of a bush or shrub of some sort. According to Phillips (1926:38) "all Scoters invariably retire to fresh water for breeding."

The Old-squaw has a marine coastal nesting distribution. Although this species is never found far from the marine coast, it most frequently nests close to fresh water. The Old-squaw nests on the ground, very often in a depression. The nest may be placed in an open, unprotected situation or in the shelter of a shrub or rock.

The golden-eyes and Buffle-head are restricted principally to inland, fresh water, forested areas during the breeding season. All three species nest in holes in trees; in Iceland (where there are no trees) Barrow's Golden-eye nests on the ground.

The Smew and Hooded Merganser, the former Palaearctic and the latter Nearctic, are both tree-nesting forms which nest inland in forested areas near fresh water.

The Goosander (Mergus merganser) also nests in holes in trees and inhabits principally inland, forested situations near fresh water. The species occasionally nests on the ground, however; its breeding distribution extends north of the tree zone, although by no means as far north as that of the Red-breasted Merganser.

The breeding distribution of the Red-breasted Merganser is not limited to fresh water (as is that of the Goosander); this species nests on the ground in marine coastal situations as well as in inland fresh water situations. The nest itself is placed on the ground and protected by a shrub or a rock; sometimes the nest is placed in a shallow depression or even a burrow.

Nothing is known of the nesting habits of the Chinese Merganser. The habitat of the bird is certainly inland and fresh water. Whether or not it nests on the ground has not been established.

Although the Auckland Islands are in part forested (Cockayne, 1909:182-235), there is good reason to believe that the Auckland Island Merganser is (or was) a ground-nesting form. Waite (1909:599) says "the domestic pig runs wild on the Auckland Islands, having been introduced in 1807... and when one has witnessed the fearlessness of so many different kinds of ground-haunting birds it is easy to comprehend how the introduction of an omnivorous animal may be an important factor in their extermination. There can be small doubt that the introduction of pigs to the Auckland Islands has already

resulted in considerable havoc among the ground-nesting birds, by destroying both eggs and young." Falla (in litt.) says "I have ascertained from older naturalists who had seen the bird that its main haunts were the narrow valleys of the many streams flowing down into the harbours along the eastern coast of Auckland Island and the north sides of Adams Island.... There are so many wild cats and pigs on the main Auckland Island that I am confident that they are extinct there."

2. Winter Habitat

Scoters.-- Cottam (1939:113) has summarized the winter ecological distribution of the scoters as follows: "although not averse to the open ocean, the scoters generally frequent the quieter waters of bays and estuaries.... Though predominantly and typically sea ducks except during the breeding season, the scoters are all noticeably less pelagic than the eiders, frequenting in limited numbers the larger inland bodies of water, such as the Great Lakes."

Descriptions of the winter habitat of the Common (or American) Scoter are contradictory. Brooks (1920:365) says "in British Columbia this scoter is an exclusively maritime duck....Not only is it a maritime bird, but it is seldom found in the small bays and inlets where the other species swarm, but frequents the exposed shores and outer reefs together with the harlequin." Cottam (1939:127) states that "the American Scoter does not seem to choose such a boisterous ocean as do the eiders, harlequins, or old squaw. It seems to prefer some protection, such as is found in coastal bays

and sounds where the water depth does not exceed 25 feet and where nature has supplied a bounteous crop of mussels." Witherby et al. (1949:348) describe wintering Common Scoters as being "exclusively marine, preferring open stretches of sea not far from coast and generally avoiding 'broken water or skerries such as are frequented by Eiders and Velvet-Scoters' (Millais)." Bent (1925:126-127) states that "the American Scoter is more often seen in fresh-water ponds a few miles back from the coast than are the other two, though all three are often seen on our large inland lakes....The waters lying south of Cape Cod and in the vicinity of Nantucket and Marthas Vineyard are particularly congenial to these birds in winter, where the numerous islands, bays, and reefs offer some shelter from the winter storms...and where they can find extensive beds of mussels, scallops, clams, and quahogs within easy reach on the numerous shoals and ledges. Here they congregate in enormous numbers, the three species associated together and often with eiders and old-squaws."

According to Grinnell, Bryant, and Storer (1918:196), the American Scoter can forage in water as deep as 40 feet. However, Dewar (1924:120), discussing 498 dives, recorded none deeper than 21 feet and "80 per cent of all dives... were referred to depths of water ranging from one to two fathoms." Dewar (1924:119) also states that Oidemia nigra is a bottom-feeder with a preference for rocky ground."

Madsen (1954:179) describes the winter habitat and diving habits of the Common Scoter as follows: "it mainly stays

out to sea and is a skilled diver which can take its food at considerable depths....the usual feeding depth would seem to be about 10 to 20 m." Madsen's food habits data (1954:179) include stomachs from Common Scoters "which are known to have foraged at depths of 20 - 30 m."

Madsen's (1954:185) study of the food habits of Common Scoters wintering on the coast of Denmark revealed that "the Common Scoter favours feeding on areas of sandy bottom where it takes immobile food species which can be directly collected on the bottom or in the most superficial layer....The Common Scoter also consumes very large quantities of blue mussels, but probably does not seek them on the submerged reefs....the Common Scoter must in general feed at some depth, and feeding at depths from 10 m to more than 20 m seems to be usual."

The White-winged (or Velvet) Scoter (Melanitta fusca) appears to have a winter habitat very similar to that of Oidemia nigra. Witherby et al. (1949:353-354) state that the Velvet Scoter is "maritime outside breeding-season like Common Scoter and often found in same places, though on the one hand perhaps more indifferent to exposed and stormy waters, and on the other more inclined, like the Eider, to frequent estuaries and vicinity of shore where muddy mussel-banks afford good food-supply..../it/ feeds largely in rocky localities and well out to sea, but also on mussel-beds close inshore, where it may mingle fortuitously with Eiders." Bent (1925:135), discussing the White-winged Scoter, says that "on the New England coast, where it is abundant in the winter, it is

strictly maritime and seems to feed mainly on small mussels and other small mollusks which it obtains by diving about the submerged ledges, often to a depth of 40 feet, tearing, with its powerful bill, the shellfish from the rocks to which they are firmly attached." Bent (1925:137-141) says further that "it dives to considerable depths for its food when necessary, though it prefers to feed at low tide when the mussel beds are nearer the surface....At certain stages of the tides, when the water is not too deep over their feeding grounds, they fly in regularly, day after day, to the same spot to feed on the mussel beds on the submerged ledges and sunken rocks along the shores and even in the harbors." Dewar (1924:116) writes that "the Velvet Scoter is mainly a bottom-feeder, especially on rocky ground. It tends to remain well out at sea, and no dives were recorded in less than four feet of water." Dewar (1924:117) analyzed 296 dives of this species and recorded none deeper than 24 feet, while most of them were two to three fathoms.

Madsen (1954:186) states that the Velvet Scoter "occurs almost exclusively in the marine habitats, but besides out to sea also often near the coasts." His specimens included "some birds which were collected when feeding in water of 14 m and 20 - 30 m depth respectively." Madsen (1954:192) states further that Velvet Scoters are "not as distinctly bound to the open sea as...the Common Scoter, but forage also, fairly frequently, nearer the coasts....it appears also that periwinkles and small crabs, which preferably live among the stones of the shallower water, constitute a greater part of

the diet of the Velvet Scoter than of the Common Scoter.... Like the Common Scoter also the Velvet Scoter favours feeding on sandy bottom....And like the Common Scoter it obtains its food easily even at such considerable depths as 20 m or more."

The Surf Scoter, according to Phillips (1926:51), "seems to be more of a sea duck even than the other two." Forbush (1925:278-279) states that the Surf Scoter "in New England is mainly a bird of the sea-coast. It feeds much along the shore outside the breakers....It is not so common as the White-winged Scoter on the shoals at long distances from the shore and is uaually rare in our interior waters." Cottam (1939:121) says of the Surf Scoter: "Although it can typically be regarded as a coastal bird, a limited number remain in the interior during the winter, particularly on large bodies of water, such as the Great Lakes. It is less inclined to drift inland than is the white-winged scoter....Although it is often seen feeding in mixed flocks of other seafowl in quiet coastal estuaries, it is not uncommon to observe it just outside the breakers..." Bent (1925:148) states that the food of the Surf Scoter "consists almost entirely of various small molluska....The large beds of the common black mussel which are so numerous and so extensive in the tidal passages of our bays and harbors or on outlying shoals are their favorite feeding grounds.... although they can dive to considerable depths to obtain food if necessary, they evidently prefer to feed at moderate or shallow depths..." Phillips (1926:52) says that "the Surf Scoter feeds in the same places as the White-wing and at the same depths, that is from six or eight to thirty feet."

Old-squaw.-- In winter the Old-squaw is mostly a marine species. Kortright (1942:286) says: "many winter on the Great Lakes and larger inland waters, but in winter they are decidedly a maritime species and congregate on the sea coasts by preference." Witherby et al. (1949:318) state that the Old-squaw is "out of breeding-season thoroughly marine, usually resting and feeding well away from shore, though sometimes close in, and seldom resorting to coastal fresh waters, though doing so regularly in small numbers in some localities; rare... on open lakes or reservoirs inland." According to Bent (1925: 43) "most of the oldsquaw's food is obtained by diving in water of moderate depths to the beds of mussels (Mytelis edulis) and other bivalve and univalve mollusks, but many of these are picked up in shallow water, as the rising tide covers the ledges....Much food is also picked up along the beaches..." Madsen (1954:194) says that the Old-squaw winters commonly in Denmark; he states that "it stays mainly out to sea, especially at night, whereas during daytime it may go nearer the coasts in order to forage. Only very rarely does it occur in the fiord areas or on the large lakes. The species is a skilled diver which usually obtains its food at depths of several metres....it may easily reach the bottom at depths of about 30 m and at times perform even considerably greater dives."

Schorger (1947:151-152) and Cottam (1939:73-74) have summarized much of the literature dealing with the depths to which the Old-squaw can dive. There is no doubt that the Old-squaw can dive to extreme depths; many individuals

have been caught in nets set at 180 feet and there are accounts (Schorger, 1947:152) of their being caught in nets set in water over 200 feet in depth.

Golden-eyes.-- Characterizing the winter habitat preferences of the golden-eyes and the Buffle-head, Cottam (1939:56) says that the three species usually frequent "large expanses of water rather than small ponds or enclosed shallow sloughs."

The Common Golden-eye (Bucephala clangula) according to Madsen (1954:205) is a common winter bird in Denmark "occurring mostly in the coastal waters of marine and brackish localities, but also visiting the large inland lakes." In North America this species "in winter...seems to prefer the coastal waters, although it is found inland in sizable numbers wherever there are large bodies of water" (Cottam, 1939:56). Witherby et al. (1949:309) state that the Common Golden-eye is "outside breeding-season mainly marine, frequenting sea-coast and tidal estuaries or river mouths and having...a liking for places where both fresh salt water are available. Also quite frequent in small numbers on larger fresh waters inland; in Scotland parties often spend whole winter on inland reaches of rivers."

The Common Golden-eye, in contrast to the scoters and the Old-squaw, does most of its diving in shallow water. Dewar (1924:111) says that about 80 per cent of the Golden-eye's dives in salt water were made in 6 to 12 feet of water; 13 feet was the maximum depth he recorded. Madsen (1954:205) states that "the Golden-Eye usually feeds at depths of about

1 to 6 m, preferring the shallow feeding-grounds...and probably... never dives in depths of more than 8 to 10m..." Madsen (1954: 220) says further that "the Golden-Eye is very adaptable in its food selection, taking not only immobile bottom animals, but also catching more mobile forms as fish and shrimps etc. The Golden-Eye dives only to moderate depths for which reason many food items taken by...the Longtailed Duck does not appear in its diet, but the Golden-Eye...frequents many different habitats and...takes a great variety of food species."

Barrow's Golden-eye (Bucephala islandica) winters on the seacoast and on large inland lakes and rivers. Cottam (1939:65), comparing the two golden-eyes states that "in habits, characteristics, and food, these two species are much alike."

The Buffle-head (Bucephala albeola), like the two golden-eyes, winters on the sea-coast and on large inland lakes and rivers. Buffle-heads gather in large numbers in shallow, coastal bays. Cottam (1939:69) says "in feeding, it seems to prefer water ranging from 4 to 15 feet deep and occurs most commonly on the larger and more open bodies of water."

Mergansers.-- The Smew (Mergellus albellus), according to Witherby et al. (1949:374), "outside breeding-season resorts to rivers, lakes, reservoirs and ponds, but very seldom to open sea. Rather fond of quite small and shallow fresh-water pools which other 'saw-bills' would avoid." Phillips (1926:234) says "the Smew is both a fresh- and a salt-water duck. In winter it is often found on the coast, preferably

in the estuaries of rivers and never in the surf or far offshore. But it is equally common on inland waters, either on the larger rivers or on good-sized lakes. It shows no liking for small bodies of water, but will, if the larger waters freeze up, take refuge even in the smallest spring."

The Hooded Merganser (Lophodytes cucullatus) is found on the sea-coast less often than the Smew. Forbush (1925:188) says it "probably rarely seeks salt water, for I have never seen it in water more salt than brackish lagoons near the sea." Phillips (1926:245) says that the Hooded Merganser "is a strictly fresh-water bird behaving in this respect quite differently from the Smew of Europe."

Comparing the habitats of the Hooded Merganser and the American Merganser, Forbush (1925:188) says "the Hooded Merganser is not ordinarily, like the Merganser, a frequenter of swift waters but seems to prefer slow streams and quiet, shaded pools. Nevertheless when wintering in the north, it goes by necessity to fast running streams, river rapids or open spring-holes..." Bent (1923:27) states: "the hooded merganser lives and feeds almost exclusively on and in fresh water; I believe that some of its food is obtained on the surface, but it is an expert diver and finds much of its food on muddy or stony bottoms. Its food is mostly animal, and consists largely of insects. Like other mergansers, it is expert at chasing and catching small fish, which probably constitute its chief supply; in muddy pools it finds frogs and tadpoles and snails, and other mollusks; on clear stony

bottoms it obtains crawfish, caddis fly larvae, and dragon-fly nymphs; sand eels, small crustaceans, beetles, and various aquatic insects are also eaten. It is also known to eat some vegetable food, the roots of aquatic plants, seeds, and grain."

The Goosander (Mergus merganser), according to Phillips (1926:264-265), "may be found on either fresh or salt water, though it is typically a bird of rivers and lakes....They frequent especially streams with clear sandy or rocky bottoms, and they seem to have no objection to rapid currents, though they like quiet pools off the main streams. They will also stay on larger lakes, but are rarely seen on muddy waters anywhere. In very severe winters they...will take refuge on any open water....They spend the whole winter on northern rivers wherever the water is rapid or warm enough to remain open." Phillips (1926:266) says further that Goosanders "undoubtedly like to fish in shallow water and soon after coming into a pond they will, if undisturbed, take to following the shoreline, keeping in water from two or three to ten or twelve feet deep. J. A. Munro (1923) clearly describes the difference in feeding and diving habits in the two species of Mergansers as seen in a large lake. Munro noticed that the American Merganser swims rapidly, with head submerged and follows the contour of the shore, three or four birds working together, and when fish are sighted, rushing along the surface with wings vigorously beating the water, with the object apparently of driving small fish into shallower water. The Red-breasted species, on the other hand, likes deeper water, and pursues a straighter course" (Phillips, 1926:266).

Of the Red-breasted Merganser (Mergus serrator) Bent (1923:21) says "on the New England coast in winter this bird is to be found in largest numbers off the beaches and in the coves and harbors. It frequents also the tidal estuaries among the salt marshes....It occasionally visits the fresh-water ponds and rivers during the migrations along the coast, but does not prefer them to salt water, as does its cousin the goosander." Phillips (1926:286) states that the Red-breasted Merganser "is a salt-water bird, although on migration it may be found almost anywhere, especially in large lakes, where a few even winter." This species, according to Bent (1923:18) "delights in the rapids of rivers, in tidal estuaries, and in the shallow places off sand beaches and at the mouth of rivers, where small fish most do congregate." Phillips (1926:288) says that "although a great deal of the food is...captured without their going to the bottom, I have watched birds which, from their constant position and regular dives in water not over ten or fifteen feet deep, seemed to be feeding largely on bottom."

The Brazilian Merganser (Mergus octosetaceus) and the Auckland Island Merganser (Mergus australis) are both non-migratory forms. Partridge (MS) has observed the Brazilian Merganser extensively in Argentina; he says that "the Brazilian Merganser seems to find the proper habitat conditions on...wild streams that flow through luxuriant tropical forest." Waite (1909:587), quoting a conversation he had with Captain Bollons concerning the Auckland Island Merganser,

says "I asked him if he did not consider it likely that the merganser had obtained the fish [Galaxias] from some fresh-water stream close to the sea. 'But why close to the sea?' said Captain Bollons. 'I have never yet seen the bird feeding close to the sea; it is always picking about in the creeks.'" Although the above is scant information, it suggests that Mergus australis was an inland, stream-dwelling merganser.

Mergus squamatus is migratory and seems to be mostly inland and fresh-water in winter distribution.

3. Diving Habits

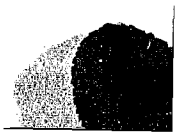
The species in the scoter - golden-eye - merganser group exhibit two methods of underwater locomotion: 1) wings and feet used as the means of propulsion (scoters and Old-squaw), 2) feet only used as the means of propulsion (golden-eyes, Buffle-head, and mergansers). Those species that generally use both feet and wings in diving do not invariably use their wings; this variation from the "normal" method of underwater locomotion may depend on the depth of the water and possibly other factors. Similarly, those species that generally use only the feet in diving sometimes use their wings as well. "Mr. Wm. Brewster...has seen [the Golden-eye] make use of its wings in diving, but this was probably at times when the bird was hard pressed..." (Townsend, 1909:241).

It is very difficult to obtain good observations of the activities of ducks under water. However, it is possible to infer some of the underwater activities from a bird's movements at submergence. Townsend (1909:234) says: "in watching

wild birds diving I have concluded that those that spread their wings just as they enter the water, use them under water, while those that keep the wings tightly pressed to the sides, and often execute graceful curves in diving, sometimes leaping clear of the water, depend on the feet alone. The truth of this conclusion I have confirmed in some instances by observing the bird under water; in other instances the conclusion has been borne out by the observation of others, so that the rule is, I think, a good one." Unfortunately, Townsend's "rule" does not take into account the fact that some birds that dive with their wings use their feet as well, while others do not.

Scoters.- The White-winged (Melanitta fusca) and Surf (M. perspicillata) scoters use wings and feet in underwater locomotion. There is some confusion in the literature about the underwater locomotion of the Common Scoter (Oidemia nigra).

Allan Brooks (1945:520-521) has given the best description of the underwater activities of the White-winged and Surf scoters: "the ordinary diving action of the White-winged Scoter is peculiar. The wings are flipped forward as the bird plunges, but under water the tips of the primaries can be seen crossed over the tail, the secondaries are somewhat expanded, showing the white patch conspicuously, but the alula is extended to its utmost, giving the appearance of small, sharp-pointed wings held out rigidly on each side during the whole period of the dive....No definite movement of the wings can be seen when the bird is submerged. As in all the diving



ducks the feet appear as huge paddles with a decided lateral action....To show how dangerous it is to be positive as to the invariability of any action, an adult female of this species always dived with her wings tightly closed and covered by the flank feathers; her mate just as invariably employed the above detailed action. The pair was watched carefully over a period of six weeks and there was no variation in their diversity. All the other White-wings that I have observed were normal in diving, with a partially open wing and the alula extended." According to Brooks, the Surf Scoter dives in the same manner as the White-winged Scoter.

My own observations of diving Surf Scoters indicate that the half-folded wings are moved with a rhythmic flapping motion, as though the bird were flying underwater, and that the feet are stroked synchronously with the wings. The tips of the primaries were not crossed over the tail as Brooks has described; rather, they were some distance from the body (directed posteriorly) and moved freely with each wing stroke. In all other particulars my observations agree with Brooks'.

Forbush (1925:279) describes the underwater actions of a Surf Scoter as follows: "the wings were held about one-third spread and perfectly rigid. Used as planes or rudders they held the bird under water and on its course while the feet drove it onward. Both feet were used at once with powerful strokes..."

White-winged and Surf scoters do not invariably dive with an initial movement of half-spread wings. I have observed

both species diving without any movements of the wings at all; Stettenheim (field notes) has recorded similar observations. When diving without use of the wings a scoter will sometimes clear the water in a high arc and disappear beneath the surface propelled by the feet alone.

Brooks (1945:522) says that "the American Scoter's diving is quite different from that of the other two species. There is no suggestion of any wing movement either before or during the dive. The wings are held tight to the body and covered by the flank feathers, with no extension of the alula." Marples (1929:45), however, records the following observation on the Common Scoter (Oidemia nigra, treated here as conspecific with O. americana): "I surprised a male Common Scoter, asleep, on the bank of the drain. He leaped into the water and dived, swimming along the drain, submerged, but quite visible in the clear water. The wings were not used for swimming, but were not entirely closed; I was surprised to see that the 'bastard' wings were completely extended during the swim. The impression I received was that the partly spread wings and the extended bastards were being used to preserve the balance of the bird."

Other observers maintain that the Common (or American) Scoter uses its wings under water. Forbush (1925:272-273) says: "it can swim a long distance under water and uses both wings and feet at need for under-water progression." Townsend (1909:241) says: "our three Scoters, -- American, White-winged and Surf Scoters -- all open their wings as they dive."

Old-squaw.-- Old-squaws use wings and feet for underwater locomotion in the same way as the scoters, a possible difference being the position of the alula during underwater flight. The only illustration I have seen of the underwater locomotion of the Old-squaw (Géroudet, 1946:244) depicts the alula as pointing posteriorly and not extended, rather than extended and pointing laterally as it is in the scoters. I have seen Old-squaws on the breeding grounds diving in shallow ponds without spreading the wings at submergence. Adams (1946:283) was able to observe the activities of an Old-squaw in shallow water as follows: "the bird was diving in a channel, close to one of the banks and in water so shallow that her back frequently showed above the surface and her feet kicked up little spouts of water. I...saw the bird's progress beneath the surface for several seconds. The beak was touching the sand all the time as if sifting it and the wings were held close to the body, which was elevated towards the rear. The feet were held behind the tail and more or less level with it, the webbed toes striking out rapidly and propelling the bird along." Hull (1914:120), watching an Old-squaw diving in deep water, says: "in this bird the movement of the wings was very plainly visible for some time as it dived obliquely in the clear water."

Golden-eyes and Buffle-head.-- Brooks (1945:518) describes the diving of the American Golden-eye as follows: "wings are never used under water but are held tight to the sides beneath the flank feathers. The tail is expanded to

its full extent and appears under water to be about as broad as the body....Under-water actions [of the Barrow's Golden-eye] are exactly as in the American Golden-eye....Under-water actions [of the Buffel-head] the same as in the Golden-eyes but with an increased agility." Alford (1920:109) says "I have on several occasions been able to watch the movements of different species, including Scaup, Golden-eye, Buffle-head, and Red-breasted Merganser, when feeding on the bottom in the more shallow parts of the bay...When descending to the bottom, all the above species use the legs as paddles, working them at right angles to the body, with wings close to the sides, and spreading the tail fan-wise to act as a rudder." Millais (1913:90), describing the underwater activities of the Common Golden-eye, wrote as follows: "In clear water it is easy to note the powerful strokes of the legs of these ducks, which seem to beat with great rapidity under water and much power. The stroke is more or less parallel to the wings; the head is held out straight in front."

Bent (1925:9) says of the American Golden-eye that "its method of diving, with wings pressed close to the sides, shows that it generally uses its feet alone. Dr. Arthur A. Allen writes to me that he has 'seen goldeneyes using their wings, half spread, when feeding normally.'" About Barrow's Golden-eye, Bent (1925:20-21) says that "they invariably try to submerge even if the water is not deep enough to cover their backs, and I have never seen them dipping as red-heads and scaups frequently do. "Millais (1913:103) says of Barrow's



Golden-eye: "whilst watching males on feed, it struck me that they were less expert than the common goldeneye, and had more difficulty in getting under water. There was more noise and splash to get under, but once below the surface they seemed to be skilled performers of the highest order." Describing the Buffle-head, Bent (1925:29) says: "under water it can swim with closed wings swiftly enough to catch the small fish on which it feeds so largely; but I believe that it often uses its wings under water for extra speed."

Mergansers.-- Brooks (1945:522) has observed the diving habits of American, Red-breasted, and Hooded mergansers and states that "no wing action of any sort when diving has been observed by the writers, although William Macgillivray and other writers have testified to the contrary. It may be that wounded birds use their wings when under water, but all three species, when diving for food, shoot along beneath the water with a streamlined contour and at a great speed. When hunting for schools of small fish, both of the larger mergansers work in a formation abreast, the heads of all the flock partially submerged with the eyes beneath the surface. On sighting fish, the whole flock plunges forward, beating the water with their wings with the obvious intention of confusing the fish or driving them into shallower water. In the midst of the commotion every bird will suddenly go under, and they can then be seen darting about, twisting and turning after their prey, without any visible wing action." Selous (1901:153-154) says that "the merganser dives like the shag or cormorant --

though the curved leap is a little less vigorous -- and swims, like them, without using the wings. His food being fish, instead of getting deeper and deeper down till he disappears, like the eider-duck, he usually swims horizontally, sometimes only just beneath the surface, and, as he comes right into the shallow inlets, where the water almost laps the shore, he can often be watched thus gliding in rapid pursuit."

Phillips (1926:235), discussing the diving habits of the Smew, says "whether or not the wings are ever used in diving still remains to be decided. Seebohm (1885) says that Smews use the wings like the Guillemot, but does not say that this is a personal observation. Hume (Hume and Marshall, 1879) saw the wings used, though not fully spread, but this was in the case of a wounded bird and means little.... I am inclined to agree with Naumann (1896-1905) and Millais (1913), who doubt whether the Smew uses its wings under water."

I have been able to find nothing in the literature on the underwater activities of the Chinese, Brazilian, and Auckland Island mergansers.

4. Food Habits

The food habits of diving ducks depend on two things: 1) habitat preferences of the ducks (water depth, salinity, bottom-type, water movement, amount of vegetation); 2) characteristics of the acceptable food organisms (availability, size, motility). Madsen (1954:250) points out that "most species of Diving Ducks have a rather wide degree of

adaptability in food selection..." In addition, he says (Madsen, 1954:250) that "among the available food items the most easily obtainable within suitable size limits are preferred....The reason...molluscs constitute so prominent a part in the diet of the Diving Ducks is...their...abundance and accessibility."

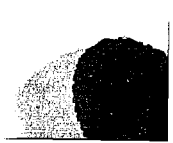
A general summary of the food habits of species in the scoter - golden-eye - merganser group follows.

Scoters.-- Cottam (1939:113) says that the scoters feed "primarily -- except during the breeding season -- on marine foods, predominantly mollusks....the scoters generally frequent the quieter waters of bays and estuaries where they find a more abundant and more accessible food supply. Their exact distribution is largely determined or influenced by the ...availability of acceptable food." Although the three scoters appear to be quite similar in their winter distributions and in the kinds of foods consumed, there are differences in the sizes of foods which they will accept and in the habitats they prefer. Cottam (1939) and Madsen (1954) point out that there are certain differences in the feeding grounds preferred by the three species of scoters. Madsen (1954: 251-252) says that the Velvet and Common scoters "take molluscs mainly 1/2 - 1 cm to about 2 cm large and prefer feeding on areas of sandy bottom, perhaps because it is more easy to find food of suitable sizes here than on the reefs. Crabs and Sea-stars are of little importance in their diet, whereas...molluscs...are eaten in great quantities. There

is a slight difference in the feeding grounds selected by the two species, since the Common Scoter stays rather exclusively out to sea whereas the Velvet Scoter also goes near the coasts and into the fjords." Madsen (1954:194) points out that "the Velvet Scoter is slightly larger than the Common Scoter, and the maximum size of the hard-shelled items it swallows appears likewise slightly larger. Bivalves as large as 4 cm...and gastropods of about 5 (maybe 6) cm... were...taken....The largest fishes consumed were...about 10 cm, and the largest worm recorded was at least 12 cm." For the Common Scoter Madsen (1954:185) says "the preferred size of the...hard-shelled molluscs seems to be from about 1 cm (0.5 - 1 cm) to about 2 cm."

Old-squaw.-- In winter the Old-squaw feeds largely on small molluscs and crustaceans. According to Madsen (1954: 205), the size of acceptable food items is 2 centimeters or less. Madsen (1954:204) states that the Old-squaw feeds on "fairly mobile animals (in part among the vegetation) in addition to picking up immobile items on the bottom..." Cottam (1939:74) says that for the Old-squaw "crustacean material serves as the chief article of food..." The Old-squaw differs from the scoters in winter food habits as follows: it depends on food animals which are in general smaller and more mobile than those on which the scoters depend; in addition, the Old-squaw is more dependent on crustaceans than are the scoters.

Golden-eyes.-- According to Cottam (1939:56) the golden-eyes and Buffle-head have much in common in food habits and



choice of diet." Munro (1939:307) says "the winter food of the American Golden-eye on coast waters appears to be substantially the same, under similar conditions of time and place, as that of Barrow's Golden-eye. While on fresh water both species feed upon salmon eggs, insect larvae, and occasionally small fish. On salt waters they eat crustaceans and mollusks and, for a short time, herring ova." Of the two species, "Barrow's Golden-eye seems to prefer fresh or brackish water to the more highly saline water....Apparently the toleration of the species for water with a highly saline content is limited and the chief wintering grounds are on the rivers and lakes....Usually it is associated with American Golden-eye but only a small percentage of the latter frequent fresh water" (Munro, 1939:287). Describing the food habits of the Buffle-head, Munro (1942:158) says "The food of chief importance on coast lakes and streams is aquatic insects....On salt water crustaceans and molluscs are about equal in times of occurrence and total percentage volume. Small fishes are of secondary importance. Herring eggs are eaten in the spring chiefly during the month of March."

Madsen (1954:220) states that the Golden-eye (Bucephala clangula) "is very adaptable in its food selection, taking not only immobile bottom animals, but also catching more mobile forms as fish and shrimps etc. The Golden-eye dives only to moderate depths for which reason many food items taken by...the Longtailed Duck [=Old-squaw] do...not appear in its diet, but the Golden-Eye...frequents many different

habitats and...takes a great variety of food species....The largest food items...have been blue mussels of only about 12 mm, and most molluscs eaten have been considerably smaller. The largest crustaceans taken have been shrimps of about 4 cm..."

The Buffle-head and the American Golden-eye seem to have very similar winter diets; I suspect, however, that the two species differ principally in size of food items they will accept and depth to which they will dive.

Hooded Merganser.-- Salyer and Lagler (1940:214), referring to Cottam and Uhler (1937), state that the Hooded Merganser "has a diet composed of a smaller proportion of fishes than the two other merganser species [Red-breasted and American mergansers]." More than fifty per cent of the diet of the Hooded Merganser is composed of insects and crustaceans; the balance consists of small fish.

Red-breasted and American mergansers.-- Differences in the winter diets of Red-breasted and American mergansers are apparently related to the habitat preferences of the two species rather than to their feeding habits. Munro and Clemens (1939:48), discussing the Red-breasted Merganser, state that "like the American Merganser this species hunts its prey by sight....When small bands of birds are fishing on salt water they swim close to shore...and their behavior after fish have been sighted is in no way different from that of the American Merganser. On the rivers also the feeding actions of the two species are identical." The American and Red-breasted mergansers have identical food habits while on fresh water (Munro and Clemens, 1939:52).

Munro and Clemens (1939:52) say that "on the sea the Red-breasted Merganser has a varied diet of marine fishes and crustaceans and in its shoreward feeding and in estuaries sometimes captures salmonoids....Probably the most important food taken in the sea is the herring..."

According to Salyer and Lagler (1940:217) the American Merganser has "a preference...for fish and other food items of the larger sizes." Salyer and Lagler (1940:192) state that American Mergansers "feed by sight and actively pursue their prey under water."

Papers by Munro and Clemens (1937 and 1939) and by Salyer and Lagler (1940) indicate that diets of the Red-breasted and American mergansers consist largely of fish; other important items are crayfish and (locally and seasonally) salmon ova. Witherby et al. (1949) state that the diet of the Goosander consists of approximately 85 per cent fish and 6 per cent crustacea, while that of the Red-breasted Merganser consists of approximately 75 per cent fish and 15 per cent crustacea.

Smew.-- Witherby et al. (1949:376) state that the diet of the Smew consists of "mainly animal matter, chiefly fish.... mostly fresh-water species...also...small crustacea...fresh-water Mollusca..." The Smew and the Hooded Merganser seem to be very similar in winter habitat and food habits.

D. Skeletal Proportions

1. Specimens

This study of the skeletal proportions of the Scoter - Golden-eye - Merganser group was based on 105 skeletons,



representing all the genera and species in the group. I was unable to examine a complete skeleton of Mergus octosetaceus or of a male Mergus australis. Specimens examined were:

Oidemia nigra americana	13	Mergellus albellus	1
Melanitta fusca deglandi	6	Lophodytes cucullatus	9
Melanitta perspicillata	4	Mergus merganser americanus	20
Clangula hyemalis	10	Mergus squamatus	1
Bucephala clangula americana	20	Mergus australis	2
Bucephala islandica	1	Mergus octosetaceus	1
Bucephala albeola	7	Mergus serrator	10

Except in the case of Mergus australis, skeletons of males only were used for this study. An incomplete skeleton of a male and a complete skeleton of a female M. australis were measured; measurements taken from the female skeleton are so marked in the accompaning tables and figures.

2. Measurements

Measurements of elements of the trunk skeleton were taken as follows: synsacrum length was measured from the anterior margin of one of the acetabula to the articulation of the anterior-most (fused) thoracic vertebra in the synsacral complex. Synsacral width was measured as the least distance between the dorsal margins of the acetabula. Thoracic length was measured as the distance between the anterior articular surface of the anterior-most thoracic and the posterior

articular surface of the posterior-most free thoracic vertebra. The anterior thoracic vertebra was distinguished from the last cervical by the absence of vertebrarterial canals. There was slight variation in the number of free thoracics; when the extra free thoracic was posterior in origin and clearly an unfused member of the synsacral complex it was measured as a part of synsacral length. When the extra thoracic vertebra was anterior in origin it was not included in the thoracic length measurement. Trunk length was computed by adding synsacrum and thoracic lengths. Sternum width was measured as the least distance between the posterior-most costal facets; sternum length is the greatest length of the body of the sternum measured along the midline. Anterior extent of the keel was computed by subtracting sternum length from keel length, which was measured as the distance along the midline from the cranial crest of the keel to the posterior-most extremity of the sternum.

The following wing elements were measured: humerus, ulna, carpometacarpus, pollex, proximal phalanx digit II, distal phalanx digit II. All measurements were of greatest length between articular surfaces. Wing length was determined by adding greatest length measurements of the humerus, ulna, carpometacarpus, and two phalanges of digit II. The combined lengths of carpometacarpus and the two phalanges of digit II are the manus length.

Montagna (1945) has presented new evidence on the homologies of the digits of the wing. If substantiated,

Montagna's evidence would require a change in the nomenclature of the digits of the wing; what is in this study called digit I, is according to Montagna, homologous to digit II of other vertebrates. To avoid confusion, I am not using here the nomenclature suggested by Montagna.

The following hindlimb elements were measured: femur, tibiotarsus, tarsometatarsus, and phalanges (except ungual) of digit III. All measurements except one were of greatest length between articular surfaces. In addition to articular length of the femur, the greatest length of the muscle scar of the external head of M. gastrocnemius was measured. This muscle scar serves as the origin of the external head of M. gastrocnemius and is on the lateral aspect of the distal part of the femur. Total leg length was computed by adding greatest articular length measurements of femur, tibiotarsus, tarsometatarsus, and phalanges of digit III. Length of digit III was computed by adding the lengths of the appropriate phalanges.

3. Method of Comparing Linear Measurements

There are two kinds of interspecific variation in the sizes of skeletal elements: variations which are correlated with the size of the organism and variations which are independent of the size of the organism. It is desirable in a study of this sort to eliminate in some way the variations due to size of the organism so that the remaining differences may be more easily studied. One way of doing this is to use

Species	Humerus			Ulna			Manus			Wing		
	Mean	σ	N	Mean	σ	N	Mean	σ	N	Mean	σ	N
Oidemia nigra	97.4	1.8	12	88.5	1.6	13	95.9	2.1	13	281.7	5.1	12
Melanitta fusca	102.3	1.7	6	91.8	1.6	6	108.6	2.9	6	302.7	5.1	6
Melanitta perspicillata	84.1	-	4	76.4	-	4	90.7	-	4	251.1	-	4
Clangula hyemalis	73.1	1.8	10	65.5	1.8	10	82.3	2.3	9	221.6	5.3	9
Bucephala clangula	82.8	1.9	20	71.5	1.5	20	85.7	1.9	17	239.9	4.7	17
Bucephala islandica	85.9	-	1	75.7	-	1	89.9	-	1	251.5	-	1
Bucephala albeola	63.8	1.6	7	55.7	1.7	7	64.6	1.5	7	184.2	4.5	7
Mergellus albellus	72.3	-	1	60.5	-	1	74.8	-	1	207.6	-	1
Lophodytes cucullatus	66.3	2.6	9	54.6	2.6	9	71.3	3.5	8	192.7	8.6	8
Mergus australis	70.9	-	1	57.8	-	1	71.1	-	1	199.8	-	1
Mergus australis *	67.0	-	1	54.7	-	1	67.4	-	1	189.1	-	1
Mergus squamatus	84.7	-	1	73.1	-	1	91.8	-	1	249.6	-	1
Mergus merganser	94.8	1.7	20	80.3	1.5	20	101.6	2.5	18	277.1	5.3	18
Mergus octosetaceus	-	-	-	-	-	-	-	-	-	-	-	-
Mergus serrator	87.6	1.5	10	73.3	1.6	10	92.1	1.6	9	253.2	4.4	9

Table 2. Mean greatest lengths of humerus, ulna, manus, and wing (male specimens except those marked *). (σ, standard deviation; N, number of specimens measured.)

Species	Femur			Tibiotarsus			Tarsometatarsus			Digit III		
	Mean	σ	N	Mean	σ	N	Mean	σ	N	Mean	σ	N
Oidemia nigra	55.3	1.0	13	90.3	2.1	13	47.4	1.3	13	67.6	1.6	13
Melanitta fusca	58.6	1.3	6	97.1	1.7	6	51.5	0.9	6	71.7	0.9	6
Melanitta perspicillata	50.3	-	4	82.3	-	4	44.5	-	4	60.3	-	4
Clangula hyemalis	42.3	0.8	10	67.6	2.2	10	35.3	1.0	10	46.5	1.5	10
Bucephala clangula	50.6	1.0	20	73.2	1.6	19	39.7	1.0	20	59.9	2.0	20
Bucephala islandica	52.1	-	1	76.3	-	1	41.3	-	1	59.0	-	1
Bucephala albeola	39.9	1.1	7	59.0	1.4	7	34.2	0.5	7	50.8	0.8	7
Mergellus albellus	41.9	-	1	63.3	-	1	33.7	-	1	48.5	-	1
Lophodytes cucullatus	39.3	2.0	9	58.5	3.0	9	31.7	1.7	9	45.4	2.3	9
Mergus australis	45.5	-	1	-	-	-	-	-	-	-	-	-
Mergus australis *	42.6	-	1	70.1	-	1	40.4	-	1	50.1	-	1
Mergus squamatus	48.3	-	1	79.8	-	1	45.0	-	1	53.5	-	1
Mergus merganser	53.3	1.2	20	89.7	1.7	20	50.4	1.1	20	61.5	2.2	20
Mergus octosetaceus	44.7	-	1	-	-	-	-	-	-	-	-	-
Mergus serrator	47.1	1.0	10	81.3	1.2	10	45.5	0.9	10	55.5	1.8	10

Table 3. Mean greatest lengths of femur, tibiotarsus, tarsometatarsus, and digit III (male specimens except those marked *). (σ, standard deviation; N, number of specimens measured.)

Species	Leg			Weight			Pollex			Sternum + Coracoid		
	Mean	σ	N	Mean	σ	N	Mean	σ	N	Mean	σ	N
Oidemia nigra	260.6	5.3	13	-	-	-	20.4	0.4	13	136.1	2.4	13
Melanitta fusca	278.8	3.7	6	1745	70	4	24.5	0.6	6	149.8	3.4	6
Melanitta perspicillata	237.5	-	4	-	-	-	21.1	-	4			
Clangula hyemalis	191.6	4.9	10	775	118	22	21.2	0.8	10	137.7	3.5	10
Bucephala clangula	223.1	4.9	19	969	116	39	17.8	0.6	20	135.8	3.2	20
Bucephala islandica	228.7	-	1	-	-	-	18.1	-	1	136.7	-	1
Bucephala albeola	183.9	2.8	7	495	60	18	12.9	0.5	7	99.7	1.8	7
Mergellus albellus	187.4	-	1	655	-	1	11.4	-	1	115.7	-	1
Lophodytes cucullatus	174.9	8.7	9	671	96	16	15.5	0.8	9	113.0	4.7	9
Mergus australis	-	-	-	-	-	-	15.0	-	1	125.8	-	1
Mergus australis *	203.2	-	1	-	-	-	14.3	-	1	114.4	-	1
Mergus squamatus	226.6	-	1	-	-	-	20.2	-	1	144.4	-	1
Mergus merganser	254.9	5.6	20	1537	190	72	21.6	0.7	20	166.1	3.4	20
Mergus octosetaceus	-	-	-	-	-	-	-	-	-	132.8	-	1
Mergus serrator	229.3	4.0	10	1075	89	11	19.5	1.0	10	143.2	5.2	10

Table 4. Mean greatest lengths of leg, pollex, and sternum + coracoid; mean weight (male specimens except those marked *). (σ, standard deviation; N, number of specimens measured.)

Species	Trunk Length Mean	σ	N	Synsacrum Length Mean	σ	N	Synsacrum Width Mean	σ	N	Sternum Width Mean	σ	N
Oidemia nigra	87.3	1.6	13	36.3	1.1	13	17.5	0.7	13	47.0	1.2	13
Melanitta fusca	97.2	1.3	6	41.0	1.4	6	22.3	0.7	6	52.7	1.1	6
Melanitta perspicillata	79.9	-	4	32.6	-	4	18.8	-	4	45.3	-	4
Clangula hyemalis	74.5	3.3	10	30.8	2.6	10	19.0	1.0	10	39.9	1.2	10
Bucephala clangula	73.3	2.7	19	26.7	2.2	19	22.6	0.9	20	42.6	1.5	20
Bucephala islandica	75.8	-	1	34.6	-	1	24.7	-	1	45.7	-	1
Bucephala albeola	55.7	1.0	7	19.4	1.3	7	16.2	0.6	7	31.1	0.6	7
Mergellus albellus	69.2	-	1	24.2	-	1	18.6	-	1	33.6	-	1
Lophodytes cucullatus	66.9	2.9	9	24.7	1.5	9	20.0	1.0	9	33.4	1.1	9
Mergus australis	83.5	-	1	34.5	-	1	18.5	-	1	40.7	-	1
Mergus australis *	77.4	-	1	32.3	-	1	17.7	-	1	36.4	-	1
Mergus squamatus	95.6	-	1	35.5	-	1	18.9	-	1	39.9	-	1
Mergus merganser	106.7	2.6	20	39.3	2.7	20	21.4	0.9	20	45.7	0.9	20
Mergus octosetaceus	81.2	-	1	31.1	-	1	18.0	-	1	37.4	-	1
Mergus serrator	93.4	3.7	10	33.6	2.0	10	16.7	1.0	10	41.3	1.7	9

Table 5. Mean lengths of trunk and synsacrum; mean widths of sternum and synsacrum (male specimens except those marked *). (σ, standard deviation; N, number of specimens measured.)

"size of organism" as a standard and express the length of an element as a proportion: length of element X 100/"size of organism." What are the most useful indexes to the size of a sea-duck?

Students of various groups of land birds (Berger, 1952; Engels, 1940; and Richardson, 1942) have used some measure of trunk length as a means of comparing all their other measurements independent of size of organism. In ducks, trunk length is clearly not a reliable measurement for this purpose. By inspection it is apparent that body length (and hence trunk length) varies considerably among the different Mergini.

Amadon (1943:167-168), discussing weight as an index of size, says: "since birds are three-dimensional objects, mass or volume as an index of general size would seem more logical than lineal measurements. In such irregularly shaped feather-clad objects, volume cannot be directly measured, but weight is easily recorded. It is an index of the mass of a bird and an indirect index of its volume, since closely related birds...may be assumed to have the same specific gravities....Differences in general size of solids will always be reflected more accurately by an index such as weight, which is proportional to the mass or volume of the object, than by any single linear measurement..." Amadon (1943:172) says further that "when weight is used as the index of general size...it is not valid to compare ratios derived from linear measurements divided by weights....Weights vary in proportion to the cube of the linear dimensions, and this



distorts the value of the ratios. The distortion could be corrected either by cubing the linear measurements or by taking the cube root of the weights. Since the object is to compare linear dimensions, the first alternative is not acceptable. Furthermore, the approximation to volumes (or weights) by cubing linear measurements has inherent difficulties, the most important one being that the error of the measurements is thereby increased (cubed). The opposite is true when cube roots are extracted....The cube root of weight may be considered to be of the same magnitude as a linear index of general size, but more reliable and usually less variable, since it is a generalized quantity (like weight itself), which is independent of variation in body form or proportions."

Clearly it would be desirable to use the cube root of weight as an index of size in this study; however, there are two difficulties involved, both of them at present insurmountable: lack of data and tremendous intraspecific variation. I have adequate weight samples for only 8 species of the 25 treated in this study. Although I have a few weight data for 14 additional species, the samples are far too small to compensate for the tremendous variation to which waterbird weights are subject. Indeed, considering the magnitude of the variation shown by the weight data of sea-ducks, perhaps none of my samples is statistically adequate. Possible sources of weight variation have been summarized by Linsdale (1928:312) as follows: "(1) the amount of undigested food in the stomachs of the individuals, (2) length of time elapsed

between shooting of the bird and taking of the weight (this allowing evaporation of the water from the body tissues), (3) general health of the bird, (4) metabolic state of the bird, and (5) instrumental error in weighing (increased when the weights are taken in the field and by different persons). The exact amount of the effect of each of these factors has not yet been determined, but it is thought that they have little effect on the names of large samples."

Although weight (or the cube root of weight) would be the most desirable index of size for this study, the great amount of variation of this measurement and the few data available make it inadvisable to use proportions of linear skeletal measurements and weights as means of comparing the linear measurements. It has been necessary to select a skeletal measurement for this purpose. I have not used sternal or synsacral measurements for the same reasons that trunk length was not used. On the grounds that the humerus exhibits the least amount of interspecific variation, I have used the humerus as a rough index of size of organism. The amount of interspecific variation in proportions of the wing is considerably less than that of the hindlimb (see Tables 7 and 8). Although using the humerus as a base measurement involves certain difficulties (see discussion of Mergus australis), I have used it on the ground that the alternatives involve even greater difficulties. A graph of mean humerus length plotted against cube root of mean weight reveals that there is a rough correlation between



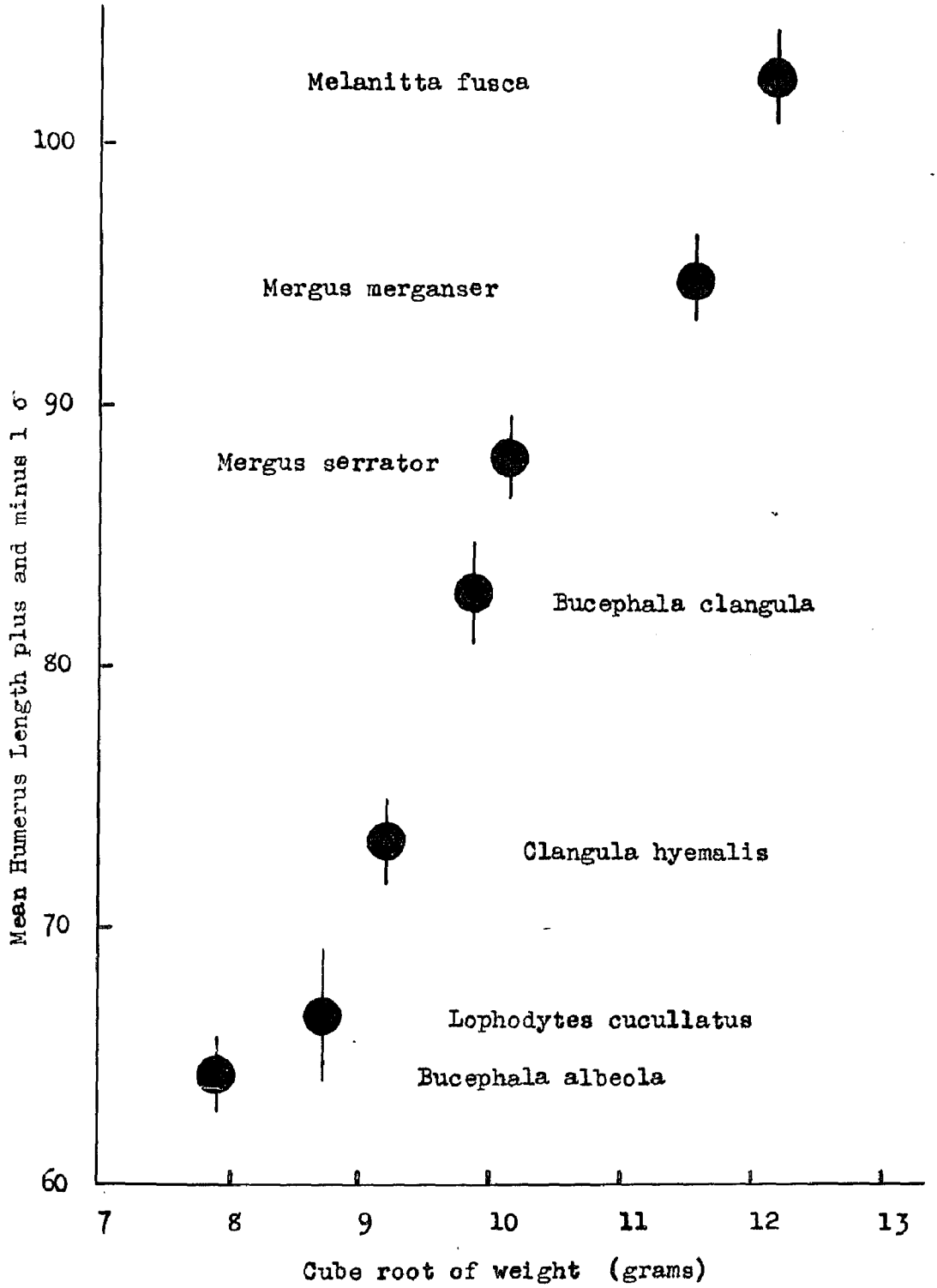


Figure 9. Mean humerus length plus and minus 1 σ plotted against cube root of mean weight.

humerus length and weight (see Figure 9). Other appendicular elements plotted against cube root of mean weight exhibit much more scatter than does the graph of the humerus: weight relationship.

4. Ratios

Engels (1940:369-370) has pointed out that there are two ways in which a ratio of the measurements of two elements may be computed: "the absolute linear measurements of a number of individuals may be averaged, and ratios determined on the basis of average measurements; or, the several ratios may be determined for each individual in the series, and the average of the ratios then determined." Table 6 compares the results of both methods of computing four different ratios for four species of diving ducks. The greatest difference in proportions computed by the two methods is 0.7 (one case); in more than three-quarters of the cases the two members of each pair of proportions differ from one another by 0.1 or less.

In the following discussion, all proportions are of the means of measurements.

5. Wing

Wing elements expressed as percentages of wing length.--Intramembral proportions of the elements of the wings of the various species of Mergini were determined by taking each element as a percentage of total wing length. It is clear from Table 7 that, among the species, the manus varies



	Manus length as a percentage of wing length				Wing length as a percentage of leg length			
	Proportion of Means	Mean of proportions			Proportion of Means	Mean of proportions		
		Mean	σ	N		Mean	σ	N
Clangula hyemalis	37.2	37.2	0.3	9	115.5	115.4	1.9	9
Bucephala clangula	35.8	35.7	0.3	17	107.2	107.2	1.6	16
Mergus merganser	36.6	36.7	0.3	18	108.8	108.7	1.6	18
Arctonetta fischeri	35.9	35.8	0.4	18	111.9	112.1	1.4	16

	Femur length as a percentage of humerus length				Synsacrum width as a percentage of length			
	Proportion of Means	Mean of proportions			Proportion of Means	Mean of proportions		
		Mean	σ	N		Mean	σ	N
Clangula hyemalis	57.9	57.9	0.9	10	61.7	61.9	5.2	10
Bucephala clangula	61.2	61.1	0.8	20	84.6	85.3	6.1	19
Mergus merganser	56.2	56.3	1.0	20	54.5	54.6	3.6	20
Arctonetta fischeri	60.1	60.0	0.9	16	61.0	61.1	4.1	18

Table 6. Comparison of the results of two methods of computing proportions.

most, the humerus least, and the ulna in between. The interspecific variation of the humerus (as a percentage of wing length) appears to be very slight; the total variation falls within a range of 2 1/2 per cent and most of it within a range of 1 per cent of the total wing length (see Table 7).

Engels (1940:368) has pointed out the difficulties of studying variations in the proportions of limb elements when these elements are expressed as percentages of the total limb length: "in considering two elements as percentages of their sum, a change in the relative percentages of the two might be the result of any one of four events: increase in the first without change in the second, decrease in the second without change in the first, relatively greater increase in the first when both are increasing, or relatively greater decrease in the second when both are decreasing; and inspection of the change in percentage would not reveal which of the four events had taken place. When three elements are involved, such as the three segments of the wing, the situation is even more complicated. I do not mean to imply that such data are without significance; such percentages express in one way the proportions of the several segments within a limb, and these proportions must be significant in the functional mechanism." Humerus length, here assumed to be more conservative than the total wing length, is undoubtedly a better standard than the wing against which to measure variations of the other elements (but see above).



Species	Humerus	Ulna	Manus
Oidemia nigra	34.6	31.5	34.1
Melanitta fusca	33.8	30.3	35.8
Melanitta perspicillata	33.5	30.4	36.1
Clangula hyemalis	33.0	29.6	37.2
Bucephala clangula	34.6	29.8	35.8
Bucephala islandica	34.2	30.2	35.8
Bucephala albeola	34.6	30.2	35.0
Lophodytes cucullatus	34.4	28.4	37.0
Mergus australis	35.4	28.9	35.6
Mergus squamatus	34.0	29.4	36.8
Mergus merganser	34.2	29.0	36.6
Mergus serrator	34.6	29.0	36.4

Table 7. Mean lengths of wing elements (humerus, ulna, manus) expressed as percentages of mean wing length (all male specimens).

Species	Femur	Tibio-tarsus	Tarsometa-tarsus	Digit III
Oidemia nigra	21.2	34.6	18.2	25.9
Melanitta fusca	21.0	34.8	18.5	25.7
Melanitta perspicillata	21.2	34.7	18.8	25.4
Clangula hyemalis	22.1	35.3	18.4	24.3
Bucephala clangula	22.7	32.8	17.8	26.8
Bucephala islandica	22.8	33.4	18.1	25.8
Bucephala albeola	21.7	32.1	18.6	27.6
Mergellus albellus	21.8	33.8	18.0	25.9
Lophodytes cucullatus	22.5	33.5	18.0	26.0
Mergus australis	21.0*	34.6*	19.9*	24.7*
Mergus squamatus	21.3	35.2	19.8	23.6
Mergus merganser	20.9	35.2	19.8	24.1
Mergus serrator	20.6	35.5	19.7	24.2

Table 8. Mean lengths of leg elements (femur, tibiotarsus, tarsometatarsus, digit III) expressed as percentages of mean leg length (all male specimens except those marked *).

Species	Ulna	Manus	Pollex	Femur	Tibio-tarsus	Tarsometa-tarsus	Digit III
Oidemia nigra	91.2	98.5	20.6	56.8	92.9	48.6	69.5
Melanitta fusca	89.5	105.9	23.9	57.3	94.8	50.3	70.0
Melanitta perspicillata	90.7	107.9	25.0	59.7	97.9	52.9	71.6
Clangula hyemalis	89.5	112.4	29.9	57.9	92.5	48.3	63.5
Bucephala clangula	86.4	103.5	21.5	61.2	88.4	48.0	72.3
Bucephala islandica	88.2	104.7	25.3	60.7	88.9	48.1	68.7
Bucephala albeola	87.4	101.2	20.2	62.5	92.5	53.6	79.6
Mergellus albellus	83.7	103.3	-	58.0	87.5	46.6	67.1
Lophodytes cucullatus	82.5	107.5	23.4	59.4	88.2	47.9	68.5
Mergus australis*	-	-	-	63.6	104.8	60.3	74.8
Mergus australis	81.5	100.3	21.2	64.2	-	-	-
Mergus squamatus	86.4	108.2	23.8	57.0	94.1	53.1	63.1
Mergus merganser	84.7	107.1	22.8	56.2	94.7	53.1	64.9
Mergus serrator	83.5	105.1	22.2	53.8	92.8	52.0	62.3

Table 9. Mean lengths of elements (ulna, manus, pollex, femur, tibiotarsus, tarsometatarsus, digit III) expressed as percentages of mean humerus length (all male specimens except those marked *).

Species	Trunk Length	Synsacrum Width	Sternum Width	Anterior Keel Extent	Sternum + Coracoid	Wing Length
Oidemia nigra	89.7	18.0	48.3	11.3	140.0	107.9
Melanitta fusca	94.9	21.8	51.5	16.3	146.1	108.5
Melanitta perspicillata	94.9	22.4	53.8	13.8	-	105.9
Clangula hyemalis	101.9	26.0	54.5	21.8	188.0	115.5
Bucephala clangula	88.5	27.3	51.5	23.3	164.0	107.2
Bucephala islandica	88.4	28.8	53.3	19.8	159.0	109.9
Bucephala albeola	87.4	25.4	48.8	17.6	156.3	100.1
Mergellus albellus	95.8	25.8	46.5	22.0	160.0	110.5
Lophodytes cucullatus	100.9	30.2	50.5	23.2	170.6	111.5
Mergus australis	117.8	26.1	57.5	24.3	177.5	94.4*
Mergus squamatus	112.9	22.3	47.1	26.7	170.7	110.0
Mergus merganser	112.3	22.6	48.2	30.6	175.4	108.8
Mergus serrator	106.5	19.1	47.1	32.4	163.5	110.4

Table 10. Mean measurements of elements (trunk length, synsacrum width, sternum width, anterior keel extent, sternum + coracoid length) expressed as percentages of mean humerus length; mean wing length expressed as a percentage of mean leg length (all male specimens except those marked *).

Distal wing elements expressed as percentages of humerus length.-- Relative sizes of the distal elements (ulna, pollex, manus) of the wings of the various species were determined by expressing the mean element as a percentage of the mean humerus length. These figures are expressed as a series of histograms in Figure 10. There are two trends discernible from Figure 10: 1) the ulna tends to be longest in the scoters and Old-squaw, shorter in the golden-eyes, and shortest in the mergansers; however, there are no clear-cut disjunctions between the groups. The difference between the shortest of the Old-squaw and scoter ulnas and the longest of the golden-eye ulnas is about 1 per cent; the longest merganser ulna is as long as the shortest golden-eye ulna. 2) the manus of the mergansers tends to be longer than that of the golden-eyes, although the shortest merganser manus (M. australis) is shorter than the shortest golden-eye manus (but see below regarding M. australis). The Old-squaw has the longest manus (112.4 per cent of humerus) and the Common Scoter has the shortest 98.5 per cent of humerus). Variations in the relative lengths of the manus in the different species show no clear correlation with variations in the method of underwater locomotion. The relatively long ulnas of the scoters and Old-squaw and the shorter ulnas of the golden-eyes and mergansers suggest that ulna length has some adaptive significance with respect to underwater locomotion. This possibility is strengthened by the fact that the eiders (which use their wings underwater) all have long ulnas (88.0 - 89.7 per cent of humerus length).

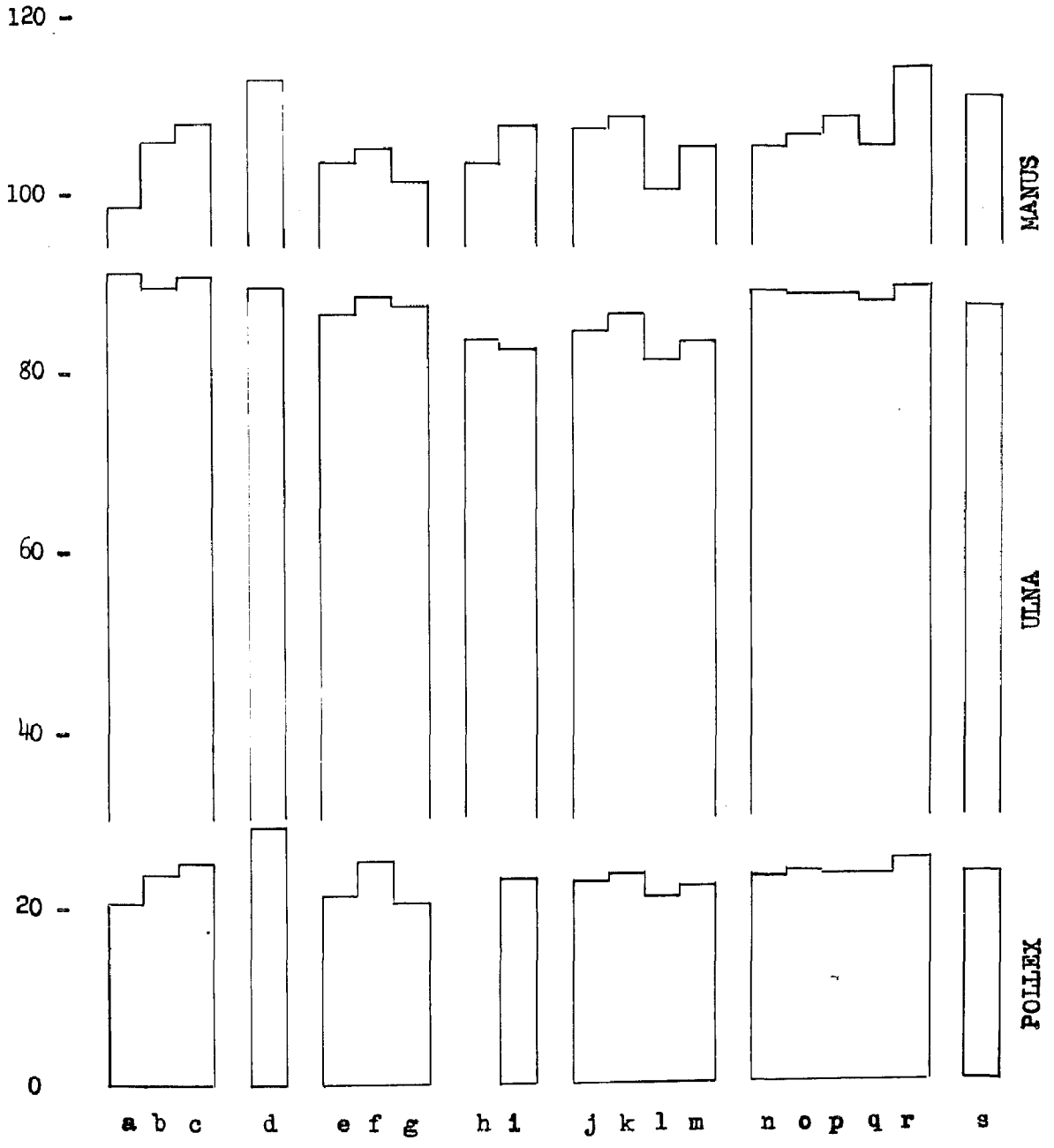


Figure 10. Histograms of mean wing element lengths (ulna, manus, pollex) expressed as percentages of mean humerus length; (a, Oidemia nigra; b, Melanitta fusca; c, Melanitta perspicillata; d, Clangula hyemalis; e, Bucephala clangula; f, Bucephala islandica; g, Bucephala albeola; h, Mergellus albellus; i, Lophodytes; j, Mergus merganser; k, Mergus squamatus; l, Mergus australis; m, Mergus serrator; n, Somateria m. v-nigra; o, Somateria m. dresseri; p, Somateria spectabilis; q, Arctonetta fischeri; r, Polysticta stelleri; s, Histrionicus histrionicus.)

However, the fact that the ulna of Barrow's Golden-eye is 88.2 per cent of the humerus (one specimen) casts doubt on the adaptive significance (with relation to underwater locomotion) of length of the ulna in these birds.

The proportions of the pollex in these species are puzzling; there is no clear-cut trend discernible (see Figure 10). The species which use their wings underwater show both extremes in development of the pollex. The size of the pollex in the species which do not use their wings underwater varies between the two extremes.

The wing proportions of Mergus australis are quite different from those of the other mergansers: the manus is considerably shorter than it is in any other Mergus, and the ulna is slightly shorter. The fact that M. australis is, or was (the species may now be extinct), a non-migratory species limited in distribution to the Auckland Islands, suggests that the whole wing may have become reduced to some extent. Since this cannot be tested in terms of the humerus, some other means of comparison must be used. Mean wing length taken as a per cent of mean leg length in the mergansers varies between 108.8 per cent and 111.5 per cent except for Mergus australis in which the wing length is 94.4 per cent of the leg length. This suggests that all the elements of the wing of M. australis have become reduced in length; the manus most of all and the humerus an undetermined amount. This idea will be elaborated further in the discussions of the proportions of the trunk and of the leg.

6. Trunk

Variations in trunk length were studied in the scoter - golden-eye - merganser group by expressing trunk length as a percentage of humerus length and comparing the resulting ratios. Examination of the histograms in Figure 11 reveals that the species of Bucephala and Oidemia nigra have the smallest trunk lengths (87.4 - 89.7); the species of Melanitta have somewhat longer trunks (94.9); Clangula hyemalis and Lophodytes cucullatus have even longer trunks (101.9 and 100.9); the species in the genus Mergus (M. octosetaceus could not be compared) have the longest trunks (106.5 - 117.8). Mergus australis appears to have the longest trunk of the mergansers (117.8); however, this is probably because of a reduced humerus in this species (see below).

Sternum and coracoid length (added together) is longest in the Old-squaw (188 per cent of humerus) and shortest in the scoters (140-146 per cent of humerus). The golden-eyes vary from 156.3 (B. albeola) to 164.0 (B. clangula); the mergansers vary from 163.5 (M. serrator) to 175.4 (M. merganser); M. australis is 177.5 (see Figure 11).

Anterior keel extent is greatest in Mergus (24.3-32.4 per cent of humerus), and least in Oidemia (11.3 per cent of humerus). Melanitta perspicillata is 13.8; Melanitta fusca and Bucephala albeola are 16.3 and 17.6; Bucephala islandica and Clangula hyemalis are 19.8 and 21.8; Lophodytes and Bucephala clangula are 23.2 and 23.3 (see Figure 11).

Trunk length, sternum plus coracoid length, and anterior keel extent vary in the same way in the scoter - golden-eye -

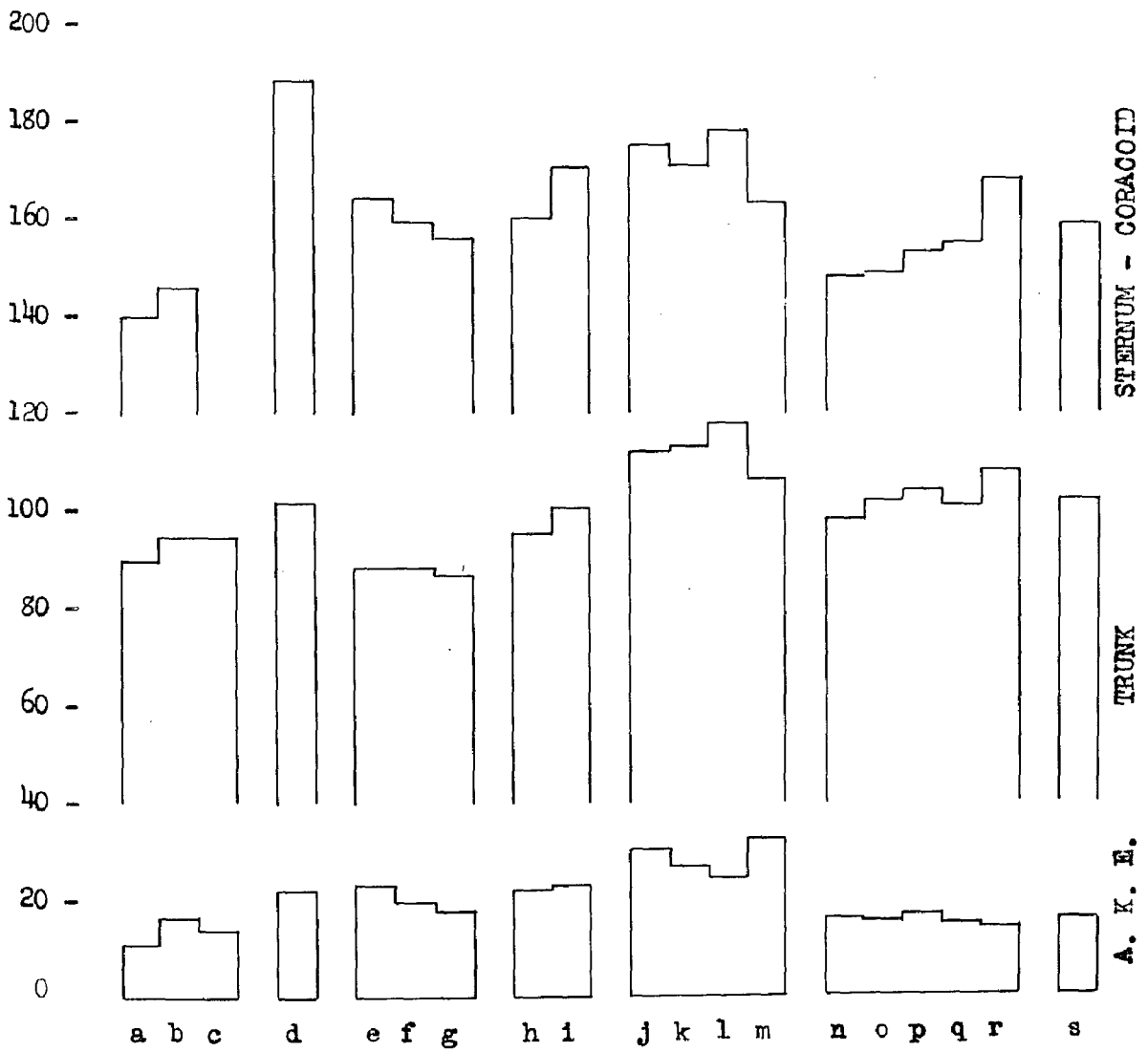


Figure 11. Histograms of mean trunk length, sternum plus coracoid length, and anterior keel extent (A.K.E.) expressed as percentages of mean humerus length. (a, Oidemia nigra; b, Melanitta fusca; c, Melanitta perspicillata; d, Clangula hyemalis; e, Bucephala clangula; f, Bucephala islandica; g, Bucephala albeola; h, Mergellus albellus; i, Lophodytes cucullatus; j, Mergus merganser; k, Mergus squamatus; l, Mergus australis; m, Mergus serrator; n, Somateria m. v-nigra; o, Somateria m. dresseri; p, Somateria spectabilis; q, Arctonetta fischeri; r, Polysticta stelleri; s, Histrionicus histrionicus.)

merganser group. In a general way, a bird that has a long trunk will have a long sternum plus coracoid length and a long anterior keel extent. There are some exceptions: Clangula, which has by far the largest sternum plus coracoid length, has a trunk length which is greater than that of the scoters, golden-eyes and Hooded Merganser but less than that of the true mergansers (Mergus); trunk length in the golden-eyes is less than in the scoters while sternum plus coracoid length and anterior keel extent are greater; anterior keel extent in Clangula is less than in Bucephala clangula but greater than that of the scoters; Lophodytes is much greater than the golden-eyes in trunk length and sternum plus coracoid length but is about the same as B. clangula in anterior keel extent.

The mergansers (Mergus) have the narrowest sterna; the Old-squaw has the widest. Melanitta, Bucephala clangula, and B. islandica have wide sterna; Oidemia, Bucephala albeola, and Lophodytes have narrow sterna, the sternum of Lophodytes being wider than those of B. albeola and Oidemia but narrower than those of the other two species of Bucephala and of Melanitta.

Synsacrum width is least in the mergansers (Mergus) and the scoters (Oidemia and Melanitta); it is greatest in the Hooded Merganser. The golden-eyes (Bucephala) and the Old-squaw (Clangula) have synsacrum widths which are less than that of the Hooded Merganser and greater than those of the scoters and mergansers (Mergus).

Variations in the shape of the body in the scoter - golden-eye - merganser group have been expressed in terms of trunk length and sternum width. It is useful to think of body shape in ducks in terms of length and cross-section area of the body.

Sternum width is perhaps not the most significant index of cross-section area. In a diving bird, decrease in the breadth of the body correlated with decrease in cross-section area is limited by the fact that a bird's stability on the surface of the water decreases with a decrease in body breadth. This suggests that with a decrease in cross-section area sternum width would vary less than some dorso-ventral measure of the thickness of the body. I attempted to take measurements of body thickness from fresh specimens of golden-eyes, scoters, and mergansers; I was unable to establish a measurement that did not vary so much in an individual as to be useless. The sternum of a bird is connected to the vertebral column by the pectoral girdle (coracoids) and by the ribs. The articulation of the anterior end of the sternum with the coracoids is not an immovable one; rather, the sternum moves about the articular surfaces of the coracoids much as a door on a hinge. Nor are the attachments of the sternum with the ribs immovable. The result is that the distance of the sternum from the vertebral column in a given individual can vary tremendously. For this reason my attempts to measure body thickness yielded no useful results.

Variations in body shape.-- The golden-eyes and scoters are short-bodied ducks with large cross-section areas. Melanitta

differs in body shape from Bucephala in greater trunk length; sternum width in the two genera is about the same relative to humerus length (except for Bucephala albeola, which has a narrower sternum). Oidemia and Bucephala albeola are very similar in body shape. In addition to having longer bodies than the golden-eyes, the scoters (Melanitta) are very much smaller in synsacral (interacetabular) width. The Old-squaw has a much longer body than the golden-eyes and scoters but has a cross-section area and synsacral width which is (relative to humerus length) comparable to those of the golden-eyes. The sternum plus coracoid length in the Old-squaw is disproportionately long but this is related to the development of a posterior xiphoid plate on the sternum. Mergellus has a trunk length which is slightly greater than that of the scoters and much greater than that of the golden-eyes; cross-section area (relative to humerus length) is much smaller than that of the scoters and golden-eyes. The synsacral width of Mergellus is less than in the golden-eyes but greater than in the scoters. Lophodytes and Mergus australis have much longer trunks and slightly larger cross-section areas than Mergellus; their synsacral widths are greater than in the golden-eyes. Mergus australis and Lophodytes are intermediate between Bucephala and the other species of Mergus in trunk length and sternum width (or cross-section area). The mergansers (Mergus, except M. australis) have the longest trunks, small cross-section areas (narrow sterna), and narrow synsacra.

7. Leg

Leg elements expressed as percentages of humerus length.--Expressed as a percentage of humerus length, the femur of Mergus australis appears to be by far the longest in the scoter - golden-eye - merganser group; this is undoubtedly a result of a short humerus rather than a long femur. Apart from this exception, the longest femora in the scoter - golden-eye - merganser group are those of the golden-eyes (Bucephala) and the Hooded Merganser (Lophodytes). The femora of the scoters (Oidemia and Melanitta) and the Old-squaw (Clangula) are much shorter than those of the golden-eyes. The femora of the mergansers (Mergus) tend to be slightly shorter than those of scoters. The femur of Mergus squamatus is a little longer than that of Oidemia; the femur of M. serrator is much shorter than that of any of the other mergansers (see Figure 13).

The species of Mergus, which have the shortest femora, have the longest tibiotarsi; the scoters and Old-squaw, which have femora slightly longer than those of the mergansers, tend to have slightly shorter tibiotarsi; the golden-eyes and Hooded Merganser, which have the longest femora, have the shortest tibiotarsi. The Buffle-head, which has a long femur, is an exception to this rule and has a tibia comparable in length to that of the Old-squaw. The relationship of femur length to tibiotarsus length can be shown by a histogram of femur length expressed as a percentage of tibiotarsus length (see Figure 12).

Scoters, golden-eyes (except for B. albeola), Old-squaw, and Hooded Merganser all have short tarsometatarsi. The mergansers (Mergus) have very long tarsometatarsi; the Buffle-head

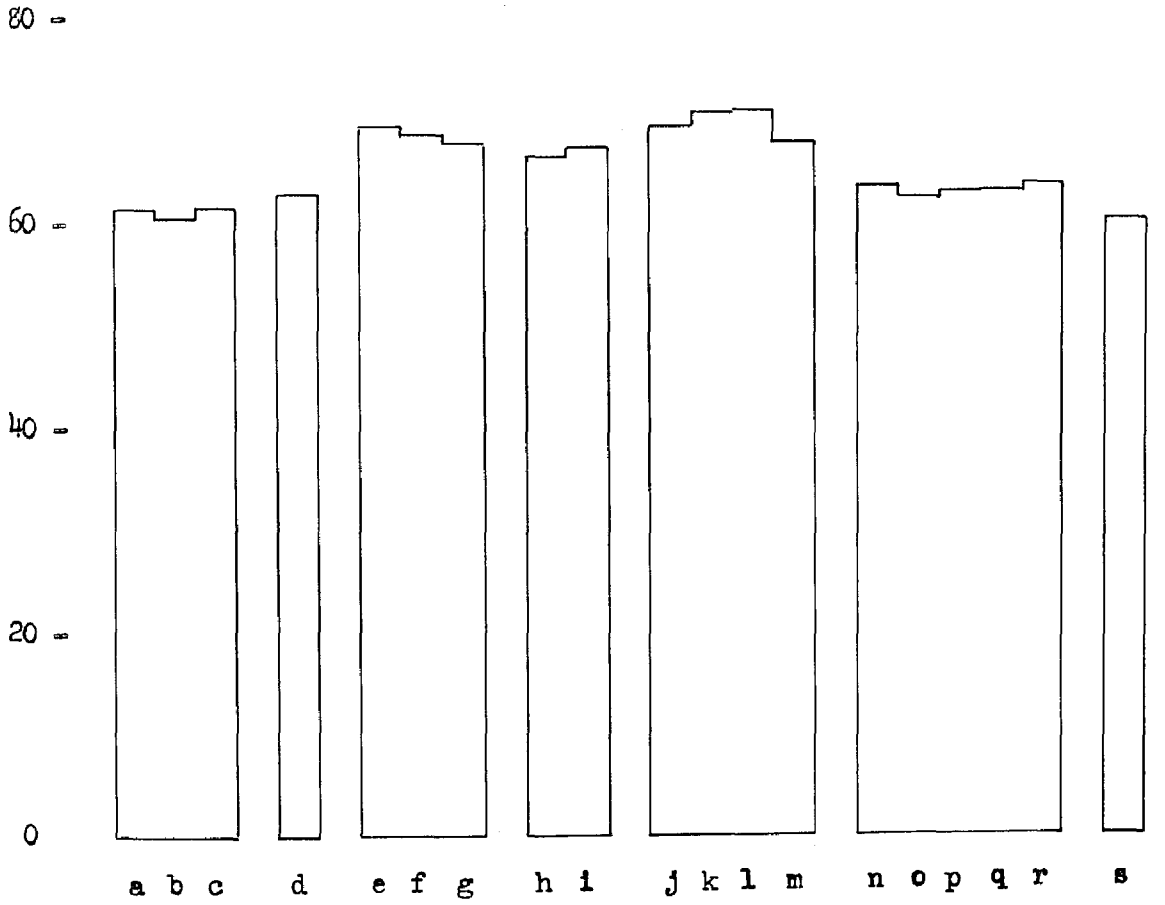


Figure 12. Histogram of mean femur length expressed as a percentage of mean tibiotarsus length. (a, Oidemia nigra; b, Melanitta fusca; c, Melanitta perspicillata; d, Clangula hyemalis; e, Bucephala clangula; f, Bucephala islandica; g, Bucephala albeola; h, Mergellus albellus; i, Lophodytes cucullatus; j, Mergus merganser; k, Mergus squamatus; l, Mergus australis; m, Mergus serrator; n, Somateria m. v-nigra; o, Somateria m. dresseri; p, Somateria spectabilis; q, Arctonetta fischeri; r, Polysticta stelleri; s, Histrionicus histrionicus.)

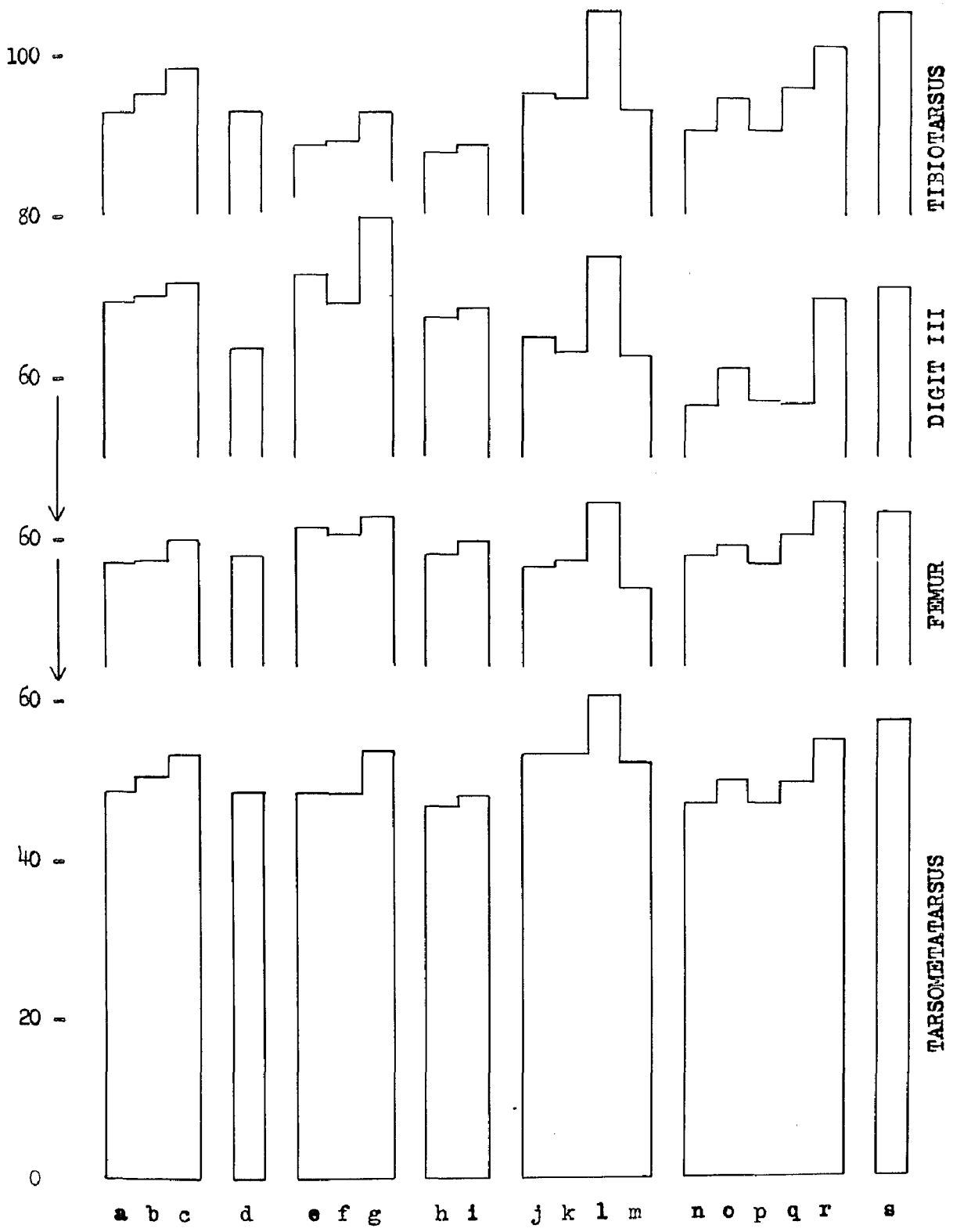


Figure 13. Histograms of mean lengths of leg elements (femur, tibiotarsus, tarsometatarsus, digit III) expressed as percentages of mean humerus length. (a, Oidemia nigra; b, Melanitta fusca; c, Melanitta perspicillata; d, Clangula hyemalis; e, Bucephala clangula; f, Bucephala islandica; g, Bucephala albeola; h, Mergellus albellus; i, Lophodytes cucullatus; j, Mergus merganser; k, Mergus squamatus; l, Mergus australis; m, Mergus serrator; n, Somateria m. v-nigra; o, Somateria m. dresseri; p, Somateria spectabilis; q, Arctonetta fischeri; r, Polysticta stelleri; s, Histrionicus histrionicus.)

has a tarsometatarsus comparable in length to those of the mergansers (see Figure 13).

There seems to be no direct relation between tarsus length and length of digit III. The variations can best be expressed as follows:

	Tarsus length	Digit III length
Bucephala albeola	long	very long
Mergus	long	short
Clangula hyemalis	short	short
Oidemia, Melanitta, B. clangula, B. islandica, Lophodytes	short	long

Bucephala albeola has by far the longest digit III combined with a tarsus length comparable to that in the mergansers.

Compared with the other mergansers (Mergus), M. australis is consistently larger in all of its hindlimb elements. By expressing the hindlimb elements as percentages of leg length, it can be seen that the mergansers (Mergus) have very similar proportions; this suggests that Mergus australis has a smaller humerus than the other mergansers (see discussion of M. australis below).

Femur and tibiotarsus.-- Variations in femur length appear to be related to diving ability or speed of underwater locomotion. The most highly specialized divers have shorter femora than the less specialized divers. Interacetabular width varies directly with femur length. The relation of interacetabular width and femur length to the diving adaptation is perhaps explicable in terms of the plane of movement

of the paddle. As the paddle passes through its arc of movement there are two components of force affecting the distal end of the tibiotarsus at the intertarsal joint. At the beginning of the stroke the component at right angles to the long axis of the tibiotarsus is very strong while the horizontal component, parallel to the long axis of the tibiotarsus, is very weak. The horizontal component increases and the component at right angles to the long axis of the tibiotarsus diminishes as the paddle moves through its arc to a point where the tarsometatarsus is at right angles to the long axis of the tibiotarsus; there, the horizontal component reaches its maximum and the right-angle component its minimum. When the arc of movement of the paddle is in a vertical plane, parallel to the sagittal plane of the animal, the right-angle component pushes the distal end of the tibiotarsus in a dorsal direction; in this situation the right-angle component contributes nothing to the forward movement of the bird. Furthermore, when the arc of paddle movement is parallel to the sagittal plane of the bird, a long tibiotarsus is disadvantageous as it magnifies through leverage the translation of the right-angle component into a dorsal movement of the posterior part of the bird. When the arc of paddle movement is in a horizontal plane, parallel to the frontal plane of the bird, the right-angle components of opposite paddles negate one another. In this situation a long tibiotarsus is not a disadvantage.

The plane of the arc of paddle movement is related in part to the position of the femur and its condyles and in

part to the orientation of the condyles of the intertarsal joint. When the femur is rotated in a transverse plane away from the body, the arc of paddle movement is moved correspondingly towards the horizontal. If a shift of the plane of movement of the paddle took place without a reduction in femur length, the protruding distal end of the femur would add materially to the cross-section area of the bird. Decrease in the interacetabular width supplements the reduction in femur length associated with a shift of the plane of paddle movement towards the horizontal.

Digit III.-- Variations in the length of digit III (which is proportional to paddle size) are related inversely to variations in trunk length. Mergus and Clangula, which have the longest trunks, have the smallest paddles. The golden-eyes and scoters, which have the shortest trunks, have the largest paddles. Mergellus and Lophodytes, which have trunks longer than the golden-eyes, have paddles which are smaller than those of the golden-eyes.

8. Humerus Reduction in Mergus australis

As pointed out earlier, most of the comparisons of elements in the scoter - golden-eye - merganser group were done by expressing each element as a percentage of the humerus; in this way it was hoped to eliminate the variations due to differences in the sizes of the various species. I am not entirely satisfied with the results of this method because in addition to the obvious case of humerus reduction in Mergus australis there are other species in which the humerus may

have undergone some reduction, particularly Bucephala albeola and Melanitta perspicillata. Because of the few weight data available for most of the species in this group it is impossible to test adequately for humerus reduction. Humerus reduction can be inferred when there are obvious differences (in one direction) between the proportions of element: humerus of one species and its close relatives. Bucephala albeola and Melanitta perspicillata are consistently larger than their close relatives in leg element and trunk element expressed as percentages of humerus length and Mergus australis is much larger in these respects. The fact that these three species have the lowest wing: leg ratios is additional evidence for wing reduction, although it is impossible to be sure that the leg is not varying to some degree.

It has been possible to establish the fact that the humerus has been reduced in Mergus australis; Mergus squamatus and Mergus merganser are so closely related to M. australis that the three forms have similar or identical proportions in the trunk and the leg. Melanitta perspicillata and Bucephala albeola do not have related species close enough (in terms of morphological and other similarities) that they can be used to test for humerus reduction.

The following facts lead me to believe that the wing of Mergus australis has become reduced:

1. Wing X 100/ Leg is 94.4 per cent in M. australis

   Wing X 100/ Leg is 110 - 111.5 per cent in Lophodytes and other species of Mergus.

2. Hindlimb elements X 100/ Humerus give much larger percentages in M. australis than in any of the other mergansers (see Table 12).

3. Intramembral proportions of M. australis show reduction of manus and ulna (as percentages of humerus) in relation to the other mergansers; the manus has diminished more in size than the ulna.

M. merganser, M. squamatus, and M. australis are very closely related -- much more closely related to one another than to any of the other mergansers. My evidence for this is principally from the structure of the trachea; other features such as plumage characteristics, position of the nostril, and skeletal proportions are also suggestive.

Mergus australis, merganser, and squamatus show little interspecific variation in the following measurements:

1. Leg length
2. Synsacrum width
3. Femur length
4. Tibiotarsus length
5. Tarsometatarsus length
6. Digit III length

In Table 11 measurements of synsacrum width and of length of leg elements are expressed as percentages of leg length. When these same measurements are expressed as percentages of humerus length, it is seen that the only exceptional proportions are those of Mergus australis in which the humerus has become reduced (see Table 12).

	Mergellus	Lophodytes	M. merganser	M. squamatus	M. australis	M. serrator
Synsacrum width	9.9	11.4	8.4	8.3	8.7*	7.3
Femur length	22.4	22.5	20.9	21.2	21.0*	20.6
Tibiotarsus length	33.8	33.5	35.2	35.2	34.6*	35.5
Tarsometatarsus length	18.0	18.0	19.8	19.8	19.9*	19.7
Digit III length	25.9	26.0	24.1	23.6	24.7*	24.2

Table 11. Measurements of synsacrum width and of length of leg elements expressed as per cents of leg length (all male specimens except those marked *).

	Mergellus	Lophodytes	M. merganser	M. squamatus	M. australis	M. serrator
Synsacrum width	25.8	30.2	22.6	22.3	26.1	19.1
Femur length	58.0	59.4	56.2	57.0	64.2	53.8
Tibiotarsus length	87.5	88.2	94.7	94.1	104.8*	92.8
Tarsometatarsus length	46.6	47.9	53.1	53.1	60.3*	52.0
Digit III length	67.1	68.5	64.9	63.1	74.8*	62.3

Table 12. Measurements of synsacrum width and of length of leg elements expressed as per cents of humerus length (all male specimens except those marked *).

By expressing each of the above five measurements (synsacrum width, femur length, tibia length, tarsus length, and digit III length) as percentages of each of the others, I have found that Mergus australis, merganser, and squamatus are very similar (practically identical) with respect to relative development of each of the parts concerned. With this fact in mind, it is possible to estimate the amount of humerus reduction in Mergus australis (see Table 13).

The calculations in Table 13 allow us to estimate that the humerus has been reduced in Mergus australis by approximately 10 to 15 per cent of its original length. It is now possible to use an estimate of unreduced humerus length as a rough index of body size in Mergus australis. I have arbitrarily selected 77.0 mm. as the unreduced humerus length of the female, and 82.0 mm. as the unreduced humerus length of the male.

Table 14 compares the skeletal measurements of Mergus squamatus, merganser, and australis; all measurements are expressed as percentages of humerus length. In the case of Mergus australis measurements are expressed as percentages of the actual humerus length and as percentages of the estimated length of the humerus before it became reduced.

Examination of Table 14 reveals that Mergus australis is smaller in the lengths of the following elements (in addition to the humerus):

1. Ulna
2. Manus

3. Pollex
4. Trunk
5. Coracoid
6. Anterior keel extent
7. Sternum plus coracoid

Because I have used proportions of leg elements and pelvis width to establish the "unreduced" length of the humerus in M. australis, I cannot reason that these same elements, expressed as percentages of the unreduced humerus length, have not undergone reduction. However, this has been established satisfactorily on other grounds; I have included the figures of these elements in Table 14 for purposes of comparison.

I have estimated the amount of humerus reduction in M. australis as between 10 and 15 per cent. Based on the assumed unreduced length of the humerus, the ulna seems to have undergone about 17 per cent reduction (when compared with M. merganser and M. squamatus) and the manus about 19 per cent reduction. Curiously, the greatest amount of reduction (about 20%) apparently took place in the length of the coracoid. The trunk length is about 11 per cent less in M. australis than in M. squamatus and M. merganser; the sternum plus coracoid length is about 13 per cent less.

The small wing and trunk proportions of Mergus australis can be interpreted with four facts in mind:

1. Mergus australis is a sedentary (non-migratory) merganser; M. squamatus and merganser are migratory.

Element X 100 Humerus	M. australis Actual % Male	M. australis Actual % Female	M. merganser and M. squamatus Expected %	M. australis Estimated unreduced humerus length Male	M. australis Estimated unreduced humerus length Female
Pelvis width	26.1	26.4	22.0 - 23.0	80.5 - 84.1	77.0 - 80.5
Femur	64.2	63.6	56.0 - 57.0	80.0 - 83.8	75.0 - 76.2
Tibiotarsus	-	104.8	94.0 - 95.0	-	73.9 - 74.6
Tarsometatarsus	-	60.3	52.5 - 53.5	-	75.5 - 76.9
Digit III	-	74.8	63.0 - 65.0	-	77.1 - 79.5
Range				80.0 - 84.1	73.9 - 80.5

Humerus length of Mergus australis: Male - 70.9 mm., female - 67.0 mm.

Calculations for male Mergus australis:

80.0 - 70.9 = 9.1 X 100/80 = 11.4%

84.1 - 70.9 = 13.2 X 100/84.1 = 15.6%

Calculations for female Mergus australis:

73.9 - 67.0 = 6.9 X 100/73.9 = 9.5%

80.5 - 67.0 = 13.5 X 100/80.5 = 16.8%

Table 13. Calculation of estimated humerus reduction in Mergus australis (expected percentages taken from Table 12).

	merganser	squamatus	australis (actual)	australis (estimated)
Ulna length	84.7	86.4	81.5 81.7*	70.5 71.1*
Manus length	107.1	108.2	100.3 100.1*	86.8 87.4*
Pollex length	22.8	23.8	21.2 21.4*	18.3 18.6*
Femur length	56.2	57.0	64.2 63.6*	55.5 55.5*
Tibiotarsus length	94.7	94.1	104.8*	91.1*
Tarsus length	53.1	53.1	60.3*	52.5*
Digit III length	64.9	63.1	74.8*	65.1*
Leg length	269.0	268.0	303.0*	264.0*
Trunk length	112.3	112.9	117.8 115.4*	101.9 100.5*
Synsacrum length	41.5	41.9	48.7 48.2*	42.0 41.9*
Synsacrum width	22.6	22.3	26.1 26.4*	22.6 23.0*
Sternum width	48.2	47.1	57.5 54.4*	49.6 47.3*
Coracoid length	72.5	77.1	68.8 65.3*	59.5 56.8*
Ant. keel extent	30.6	26.7	24.3 23.9*	21.0 20.8*
Sternum + coracoid l.	175.4	170.7	177.5 171.0*	153.1 148.8*
Coracoid basal width	23.4	25.0	27.1 24.6*	23.4 21.4*

Table 14. Comparison of elements expressed as percentages of humerus length in three species of Mergus (all male specimens except those marked*).

2. Mergus australis has existed for a long time as a very small population; it is known only from the Auckland Islands and has never been recorded there in large numbers.

3. Mergus australis, judging from the similarity of its hindlimb proportions to those of M. merganser and squamatus and its shorter trunk, has probably not become a more specialized diver than its two close relatives.

4. Mergus australis is probably more similar to the common ancestor of squamatus, merganser and australis, than are its two close relatives; the only evidence for this is the structure of the trachea, various plumage characteristics, and its relict, southern hemisphere distribution.

I think that the reduction of the wing elements of M. australis is best explained in terms of the non-migratory nature of the species. Decrease in the use of the wings, and associated reduction of the wing elements, has been demonstrated by Engels (1940) for thrashers. Other authors have shown that of two closely related species, one migratory and the other sedentary, the sedentary one has smaller wing elements (in relation to body size). I do not think that the reduction of wing elements of M. australis has been accentuated by any tendency towards perfection of the diving adaptation. If it had been, one could expect the reduction to have gone much further. A strong selection pressure towards wing reduction (related to development of the diving adaptation) coupled with small population size would undoubtedly



have allowed rapid evolution of a highly specialized diving adaptation along with a greatly reduced wing. If this had been the case, I think one could expect some hindlimb modifications to have occurred; also one would expect a long trunk rather than a short one. The short trunk of Mergus australis is possibly a heritage character associated with the primitive nature of the species rather than related to the reduction of the wing and coracoid.

E. Adaptive Radiation and Relationships

1. The Diving Adaptation in Ducks

In a consideration of the diving adaptations of the species in the Tribe Mergini, the underwater speed the birds can attain is of great interest. Increase in speed of underwater locomotion may be an adaptation for 1) pursuit of fast-moving prey, or 2) increasing the depth at which food can be obtained from the bottom without increasing the length of time spent under water. There are two important variables that must be studied in order to understand the diving adaptations of the different species of Mergini. These are:

1. The frictional forces acting opposite to the forward movement of the bird. The aggregate of these forces is known as "drag."

2. The power source, i.e., the muscles responsible for propulsion, the lever systems which translate their contractions into propulsive movements, and the webbed feet (paddles) and/or wings.

The maximum underwater speed a bird can attain is governed by the physiological characteristics of the muscles responsible for the propulsive movements of the limbs. For a bird to move underwater at a given speed, the bird's power source must be sufficient to overcome the drag that develops at that speed. Hence, the bird's forward speed is limited by the maximum power the bird can generate, i.e., the product of the maximum force per muscle contraction and the maximum frequency of muscle contraction.

The only way in which the two variables, drag and power, can be determined conclusively is by actual measurement. For drag this would entail tests in which the bird would be pulled at varying velocities through a tank of water and the drag measured for different velocities. Similar tests would have to be performed on the paddle. To determine the capabilities of the muscles, physiological tests would have to be performed to measure velocity of contraction under various load conditions. I have performed none of these tests. However, by considering some of the factors related to drag, it is possible to compare the species of Mergini with respect to their adaptations to speed under water.

The underwater locomotion of a duck can be considered in terms of pushing a body of a particular surface area through the water. The feet (and/or the wings) -- and the muscles responsible for their propulsive movements -- are the means of propulsion. The force (drag) acting on this

body as it moves through the water is essentially the product of the "effective surface area" of the body and its velocity. The "effective surface area" of a duck moving through the water can be expressed as the cross-section area of the duck times some constant (A·K). Since power is the product of force and velocity, the power required to move the body through the water will be the product of the "effective surface area" of the body and the square of its velocity:

$$\text{Power} = v^2 \cdot A \cdot K$$

The velocity of the body as it moves through the water is:

$$\text{velocity} = \sqrt{\frac{\text{Power}}{A \cdot K}}$$

If we consider two ducks, both capable of generating the same amount of power, and one of them having a cross-section area larger than that of the other, the one with the larger cross-section area will have the lower velocity. If one does not consider the physiological limitations of the power source (muscle), it is clear that differences in paddle and/or wing area will not affect the forward velocities of the two birds. We have assumed that both ducks have the same power potentialities and hence are capable of doing the same amount of work per unit time. In terms of the foot, this means that as paddle area decreases, frequency of paddle strokes will increase proportionately and the amount of power expended per unit time will remain the same. Similarly, variations in the lever system of the

paddle (assuming power constant and no muscle fatigue) will have no effect on the forward velocities of the two birds.

Variations in the following skeletal proportions seem to be related to the drag characteristics of the ducks in the Tribe Mergini: sternum width (cross-section area), trunk length, femur length, synsacrum width. I have shown (see "Skeletal Proportions") that small cross-section area, long trunk, short femur, and narrow synsacrum are structural adaptations to fast underwater locomotion.

In terms of the power source, the following variations affect the speed of underwater locomotion: 1) the number of pairs of appendages which are used as the means of underwater propulsion, and 2) the characteristics of the muscles which cause the propulsive movements of the pair (or pairs) of appendages which are used as the means of underwater propulsion.

I am unable to compare the species of Mergini with respect to the physiological characteristics of their hindlimb muscles; however, Ruck's study (1949) of the pelvic musculature of ducks includes comparisons of the relative muscular development of the hindlimbs of six genera of Mergini (Bucephala, Clangula, Histrionicus, Melanitta, Lophodytes, Mergus). Ruck states that "Mergus merganser has the most strongly developed pelvic musculature of any species... [he studied] ....Lophodytes cucullatus in this respect is no more strongly developed than the mallard." Among the other species that Ruck studied, variations in

the development of the hindlimb musculature were "trivial."

It is interesting to note that the deep-diving species in the scoter - golden-eye - merganser group (Oidemia, Melanitta, Clangula) use their wings and their feet, the shallow-divers (Bucephala) use only their feet, and the species (at least Mergus merganser) that actively pursue their prey under water have very strongly developed hindlimb musculature.

2. Origin and Development of the Diving Habit in Ducks

The first development of the diving adaptation in ducks probably arose as a clumsy modification of the surface-feeding adaptation. It is easy to visualize a dabbling duck, dependent on bottom-dwelling plant or animal food, increasing its feeding range by utilizing food resources in deeper water. One way in which the problem of feeding in deeper water has been solved (in the adaptive sense) is by the development of a long neck. This is apparently what happened in the evolution of the swans. The other adaptive solution to the problem of feeding in deeper water is diving.

Surface-feeding ducks are buoyant animals; the initial step in the development of the diving adaptation was probably overcoming buoyancy. The bird's buoyancy would make submerging and staying underwater difficult; all the bird's locomotor resources -- wings and feet -- would have to be used to overcome the tendency to float. On the rare occasions that surface-feeding ducks (Anas) dive, they use both

wings and feet. The problem of overcoming buoyancy is made more difficult in dabbling ducks by the fact that their legs are located farther forward on the body. The most efficient position for the paddles in underwater propulsion is as far posterior as possible, where they will directly counteract the upward force of buoyancy.

The first stage in the evolution of the diving adaptation in ducks probably involved the use of wings and feet as the means of underwater propulsion. Furthermore, at the same time there was doubtless some reduction of the bird's buoyancy. Once the first stage in the development of the diving adaptation was attained there were three possible directions for further adaptation:

1. Continued use of both wings and feet as the means of underwater propulsion.

2. Development of a diving adaptation in which the wings alone are used as the means of underwater propulsion.

3. Development of a diving adaptation in which the feet alone are used as the means of underwater propulsion.

There is an interesting relationship between breeding distribution and diving habits of different groups of diving birds. With the exception of the Pelecaniformes, those diving birds which are marine coastal in breeding distribution and predominantly marine in total distribution use only their wings as the means of underwater propulsion.

Likewise, those groups of birds which are inland and freshwater in breeding distribution use only their feet as the means of underwater propulsion. Examples of marine divers which depend on their wings for underwater locomotion are the Alcidae, Spheniscidae, Pelecanoididae, and eiders. Inland, freshwater divers which depend on their feet for underwater locomotion are the Colymbidae, Gaviidae, and most diving ducks. This correlation between distribution and diving habit is difficult to understand when we realize that many diving birds which are inland and freshwater in breeding distribution and depend on their feet for underwater locomotion, winter in great numbers on the marine coast. In groups other than ducks the converse of this is not true; no marine birds which depend on their wings for underwater locomotion winter in any numbers in inland, freshwater situations.

It is tempting to assume that when the diving adaptation has evolved in a marine environment the wings have become the important means of underwater propulsion, and that when it has evolved in an inland, freshwater environment the feet have become the important means of underwater propulsion. Lacking any other working hypothesis, I shall use the above assumption in discussing the adaptive evolution of the eiders and of the scoter - golden-eye-merganser group.

That all the members of the scoter - golden-eye - merganser group are primarily adapted to a method of underwater locomotion that relies principally on the feet as the means of propulsion is reflected by the fact that they all have femora which are strongly flexed and which have a large scar for the origin of the femoral head of the gastrocnemius muscle. This is also true of grebes and loons; it is not true of penguins, alcids, or eiders.

The Old-squaw and scoters habitually use both wings and feet as the means of underwater propulsion. The extent to which the scoters use their wings for underwater locomotion varies considerably. Sometimes the wings are not used at all, sometimes they are partly extended but not used for propulsion, and sometimes they are used (along with the feet) as the means of underwater propulsion. The Old-squaw uses its wings (as well as its feet) for underwater locomotion much more consistently than the scoters, although in shallow water it uses only its feet when diving. The Old-squaw and scoters have the following in common:

1. They habitually dive to great depths.

2. They winter principally on the sea-coast but also on the Great Lakes.

3. They nest near fresh water even though part (in some cases all) of each of their breeding ranges is near the marine coast.

4. They invariably use their feet for diving,

whether or not the wings are used.

5. Except during the breeding season, they are rarely seen on shallow, inland bodies of water.

It may be that the wings are of special adaptive value in certain water conditions (perhaps most often encountered in marine situations), and/or that they are useful in diving to great depths. Remembering the freshwater habits of the birds during the breeding season and that there seems to be some correlation between the marine environment and the development of a diving adaptation in which the wings are used as the sole means of locomotion, I suggest that the scoters and Old-squaw went through the early development of the diving adaptation in a freshwater environment and developed a method of underwater locomotion which depended largely on the feet as the means of propulsion. Although probably very important in the initial development of the diving adaptation, use of the wings (in addition to the feet) as the means of underwater propulsion was probably an inefficient means of locomotion in shallow, fresh waters in which there was any growth of vegetation. For this reason there may have been an adaptive emphasis on the use of the feet alone early in the development of the diving adaptation in fresh water. An early invasion of a marine and/or a deep-water habitat might account for the development of a method of underwater locomotion which used the wings as a means of propulsion. It is probable that the scoters and Old-squaw had developed, prior to invading a marine and/or



deep-water habitat, a method of underwater locomotion which did not involve the wings at all; development of a diving adaptation which depended on the feet alone had not progressed so far that an auxiliary source of power was unnecessary when invading a habitat which presumably taxed the diving powers of the birds.

The golden-eyes and mergansers use only their feet as the means of underwater propulsion. The principal difference between the two groups is that the golden-eyes are adapted to bottom-feeding in shallow water while the mergansers are adapted to feeding on moving prey -- fish. This difference is essentially one of speed of underwater locomotion; clearly the skeletal proportions of the mergansers -- and the greater muscular development of their hindlimb -- reflect their ability to move swiftly underwater. The close relationship of the golden-eyes and mergansers, plus the fact that in skeletal proportions and feeding habits the Smew and the Hooded Merganser are intermediate between the golden-eyes and the "true" mergansers, leads me to believe that the "merganser adaptation," i.e., swift pursuit of moving prey, arose from a shallow-water, bottom-feeding adaptation. A comparison of the food habits of the golden-eyes, Hooded Merganser, and the "true" mergansers reveals that:

1. In the diet of the golden-eyes, molluscs and crustacea are of about equal importance; golden-eyes also take small numbers of fish.

2. In the diet of the Hooded Merganser, fish and crustaceans (plus insects) are of about equal importance.

3. In the diets of the Red-breasted and American mergansers, fish are of great importance; these two mergansers take only small numbers of crustaceans.

Although I am only able to characterize the food habits of the golden-eyes and mergansers in the crudest terms, I think that the change in emphasis from immobile bottom-living molluscs to relatively slow-moving crustaceans and finally to swift-moving fish suggests the probable evolutionary development of the merganser adaptation to speed from the shallow-water bottom-feeding adaptation of the golden-eyes.

3. Relationships

There are three major diving adaptations in the scoter - golden-eye - merganser group:

1. Shallow water, bottom-feeding; feet only used as the means of underwater propulsion (*Bucephala*).

2. Active pursuit of fast-moving prey (fish); feet alone used as the means of underwater propulsion (*Mergus*).

3. Deep water, bottom-feeding; wings and feet used as the means of underwater propulsion (*Oidemia*, *Melanitta*, *Clangula*).

In terms of their structural adaptations to diving, the species of *Bucephala* are perhaps the least specialized (short trunk, large cross-section area, long femur, wide



synsacrum, short tibiotarsus), and the species of Mergus most specialized (long trunk, small cross-section area, short femur, narrow synsacrum, long tibiotarsus). Oidemia, Melanitta, and Clangula are more specialized than Bucephala and not as specialized as Mergus. Oidemia and Melanitta are similar to Bucephala in trunk length and cross-section area, but have shorter femora and narrower synsacra. Clangula is similar to Bucephala in synsacrum width and cross-section area but has a shorter femur and a longer trunk.

From the scoters through the Old-squaw and golden-eyes to the mergansers there is a progressive increase in complexity of structure of the trachea (including the tracheal bulla and bronchi) and of plumage patterns (including those both of adults and downy young).

Oidemia nigra is the least complex of any of the members of the scoter - golden-eye - merganser group in the following respects:

1. Males lack a tracheal bulla (type-1 condition).
2. The bronchi in males are close to one another.
3. White pattern on secondaries and coverts is lacking in both sexes.
4. Downy young lack dorsal body and wing markings.
5. Head pattern of downy young consists of dark cap and contrasting light cheek.

Melanitta fusca and Melanitta perspicillata are somewhat more complex with respect to tracheal structure and



plumage patterns than Oidemia nigra; they have the following characteristics:

1. Males have a tracheal bulla (type-2 condition).

2. Bronchi in males are close to one another.

3. White pattern on secondaries and coverts lacking in M. perspicillata and present in M. fusca.

4. Downy young of M. perspicillata lack dorsal body and wing markings; three (sometimes two) pairs of markings are present but inconspicuous in M. fusca.

5. Head pattern of downy young consists of dark cap and contrasting light cheek.

Clangula hyemalis is very similar to the scoters in several respects; it has the following characteristics:

1. Males have a tracheal bulla (type-3 condition).

2. Bronchi in males are close to one another.

3. White pattern on secondaries and coverts lacking in both sexes.

4. Downy young lack dorsal body and wing markings.

5. Head pattern of downy young consists of dark cap and contrasting light cheek.

I believe that Clangula is more closely related to the scoters than it is to any other ducks and that it evolved from a scoter-like ancestor early in the history of the scoter - golden-eye - merganser group. It is interesting to note that the Old-squaw and scoters are all deep-water, bottom-feeding birds that use their wings and feet as the means of underwater propulsion. In addition,



they are all ground-nesting birds. The differences in skeletal proportions between the Old-squaw and the scoters plus the fact that the Old-squaw seems to be more consistently dependent on its wings for underwater locomotion in deep water lead me to believe that the Old-squaw diverged from the scoter-like ancestral stock and became adapted to deep-water and/or marine conditions independently of the scoters.

The three species of Bucephala are more complex in trachea structure and plumage pattern than the scoters and the Old-squaw but have several features in common with them:

1. Mid-tracheal swelling (lacking in B. albeola).

2. Head pattern of downy young consists of dark cap and contrasting light cheek.

3. In common with Clangula, the species of Bucephala have type-3 tracheal bullas; however, the right chamber of Clangula is more scoter-like than Bucephala-like.

Other characteristics of the species of Bucephala are:

1. The bronchi in males are widely separated.

2. White pattern on secondaries and coverts prominent in both sexes.

3. Downy young have three pairs of conspicuous dorsal body and wing markings.

The Smew, Mergellus albellus, seems to form a link between the golden-eyes and mergansers. It has the follow-

ing characteristics:

1. Males have a tracheal bulla (type-3 condition).

2. Bronchi in males are widely separated from one another.

3. White pattern on secondaries and coverts prominent in both sexes.

4. Downy young have three pairs of conspicuous dorsal body and wing markings.

5. Head pattern of downy young consists of dark cap and contrasting light cheek.

6. Downy young identical in appearance with those of Bucephala. Mergellus has the tracheal bulla of a merganser and the downy young of a Bucephala. In feeding habits and proportions it is intermediate between the golden-eyes and "true" mergansers.

Lophodytes is much less Bucephala-like than Mergellus. In proportions and feeding habits, Lophodytes is intermediate between Bucephala and the "true" mergansers. However, both the tracheal bulla and the downy young are merganser-like rather than golden-eye-like.

The "true" mergansers have the following characteristics:

1. Males have a tracheal bulla (type-3 condition).

2. Bronchi in males are widely separated from one another.

3. White pattern on secondaries and coverts prominent in both sexes.



4. Downy young have three pairs of conspicuous dorsal body and wing markings.

5. Head pattern of downy young consists of dark cap and a partly or entirely rufous cheek. M. merganser and M. serrator both have dark malar streaks.

The golden-eyes and mergansers have much in common. Mergellus is intermediate between the two groups of species. Both groups are very similar in plumage patterns, behavior, and structure of the trachea. Furthermore, in feeding habits and structural adaptations to underwater locomotion the mergansers are clearly derived from a stock that structurally and behaviorally must have been very similar to the present day golden-eyes.

The structure of the trachea, plumage patterns, and nesting habits of the scoters lead me to believe that they most closely resemble the ancestral stock of the scoter - golden-eye - merganser group. The golden-eyes and mergansers are much more specialized than the scoters in structure of the trachea (particularly the tracheal bulla), plumage patterns, and nesting habits. In terms of the diving adaptation, the golden-eyes are structurally and behaviorally the least specialized members of the scoter - golden-eye - merganser group. In the evolution of the diving adaptation, the scoters and Old-squaw probably developed from scoter-like ancestors which had diving habits similar to those of the golden-eyes.



F. Genera

1. Scoters

Miller (1926) maintained that the genera Oidemia and Melanitta should be retained and further that Melanitta should be divided into the two subgenera Melanitta (including fusca, deglandi, and carbo) and Pelionetta (including perspicillata). His evidence for this view is variations in the structure of the trachea and variations in the length of the intestinal caeca.

I have studied the differences in form of the trachea among the species of scoters and find that, except for Melanitta perspicillata, the variations which Miller has described seem to be constant. The trachea of Melanitta perspicillata varies in the relative development of the mid-tracheal swelling. The extremes in the development of the mid-tracheal swelling in M. perspicillata approach on the one hand the condition found in M. deglandi and on the other hand the condition found in M. fusca. I am unable to say whether there should be one, two, or three species of white-winged scoters; series of specimens (skins and tracheas) must be studied before this question can be resolved. I do not feel that the differences between M. perspicillata and M. fusca (including "carbo" and "deglandi") warrant their subgeneric distinction.

Although the difference in trachea structure between Melanitta and Oidemia is an important one (Oidemia lacks a



tracheal bulla and mid-tracheal swellings), I think the relationships of the scoters can best be shown by placing them in a single genus (to indicate similarities) and two subgenera (to indicate differences). The plumage patterns of the downy young support this view as do certain behavioral similarities (nesting habits, diving habits, etc.). I am unable to interpret the variations in the length of the intestinal caeca (those of "Oidemia" are short and those of "Melanitta" are long); these require further study.

2. Golden-eyes

Bucephala albeola differs from the other two species in the genus in structure of trachea, tracheal bulla (all of them, however, are type-3), and bronchi, and in plumage patterns of female and head of male. The three species of Bucephala are similar in plumage pattern of downy young and in nesting habits. The species of Bucephala have similar diving and feeding habits and probably to a large extent replace one another ecologically, although more data are needed on this last point.

In spite of the structural differences between the Buffle-head and the golden-eyes, I think that the relationships of the three species are better shown by retaining them in a single genus.

3. Mergansers

The seven species of mergansers were placed by Delacour and Mayr (1945:35) in the genus Mergus because those authors could not "see any good reason for a generic division of the merganser group." Von Boetticher (1952:92) also grouped all the mergansers in Mergus but divided the genus into six subgenera as follows:

Mergus (Albellus) albellus
Mergus (Lophodytes) cucullatus
Mergus (Merganser) merganser
Mergus (Mergus) squamatus
Mergus (Mergus) serrator
Mergus (Promergus) australis
Mergus (Prister) octosetaceus

Variations in the structure of the trachea among the seven species clearly indicate that Mergellus, Mergus australis, M. squamatus, and M. merganser are more closely related to one another than any of them are to Lophodytes, M. octosetaceus, or M. serrator. The tracheal bullas of M. merganser, M. squamatus, and M. australis are practically identical; the three species are also very similar in many of their skeletal proportions, although M. australis is certainly the least specialized in some respects. The tracheal bulla of Mergellus has the basic features of the M. merganser bulla; the bullas of M. australis, M. squamatus, and M. merganser could very easily have been derived from that of Mergellus. On the other hand, the bulla of

M. octosetaceus bridges the morphological gap between the bullas of Lophodytes and M. serrator. The lack of skeletal material of M. octosetaceus makes comparison of its proportions with those of M. serrator impossible. The tracheal bullas of Lophodytes, M. octosetaceus, and M. serrator are structurally quite different from those of Mergellus, M. merganser, etc.

The position of the nostril has been used as a "key" character to distinguish females and downy young of M. serrator from those of M. merganser. This nostril difference is consistent between the two groups of mergansers; the distance from the anterior margin of the nostril to the tip of the bill is short in the Mergellus - M. merganser group and long in the Lophodytes - M. serrator group. In addition, the general proportions of the bill (short and stocky in the Mergellus - M. merganser group and long and slender and slightly recurved in the Lophodytes - M. serrator group) are consistently different between the two groups.

The courtship attitudes of Mergellus and Lophodytes have much in common with those of the golden-eyes. The courtship attitudes of M. serrator and M. merganser have very little in common with each other; the display of M. merganser is reminiscent of that of the golden-eyes; the bizarre display of M. serrator is not at all suggestive of golden-eye courtship.

There are several ways in which the relationships of the seven species of mergansers can be expressed nomen-

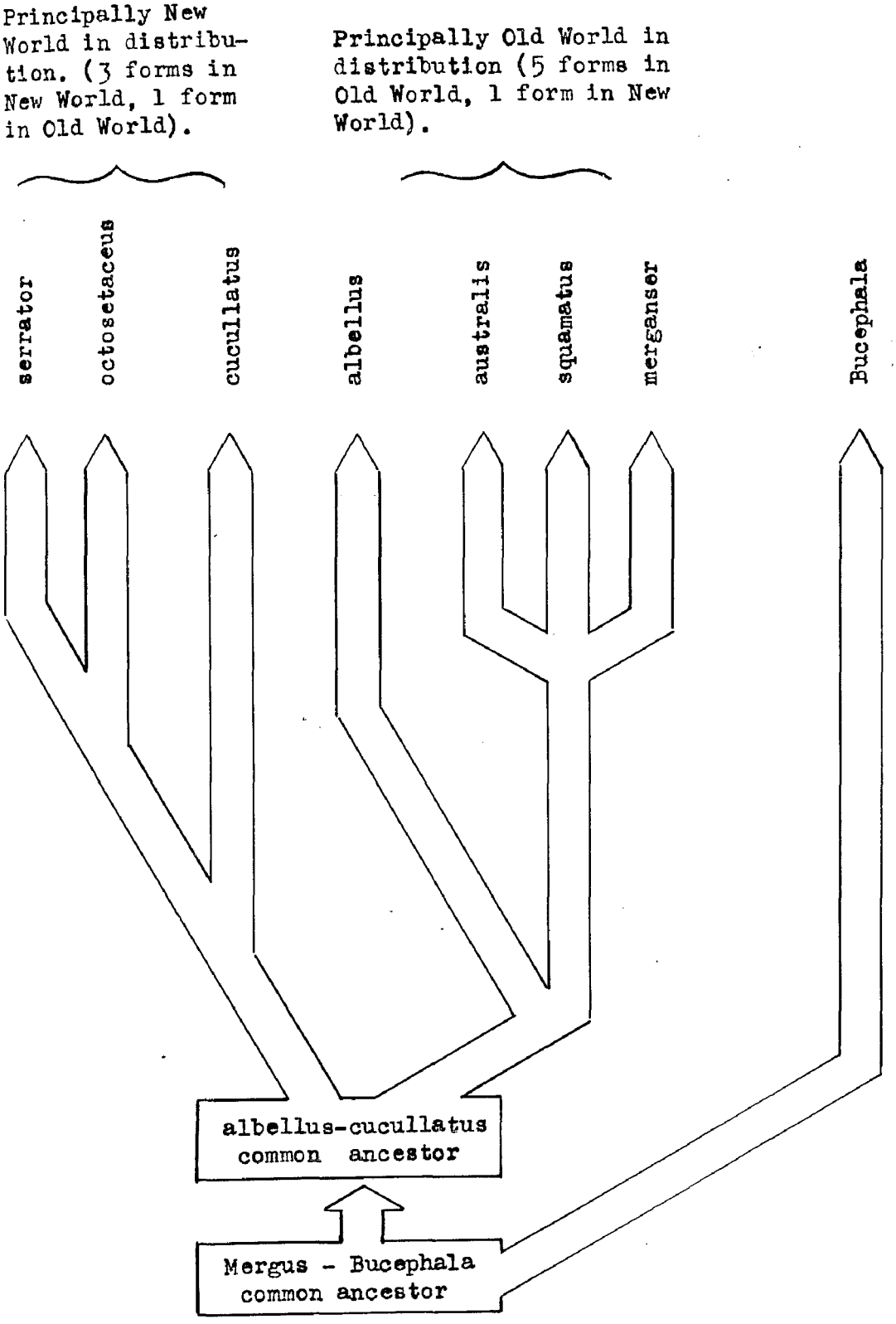


Figure 14. Diagram of hypothesized relationships of species within the genus Mergus (see text).

clatorally. A classification scheme should reflect as well as possible the relationships of species and groups of species. Delacour and Mayr's convenient solution to the merganser problem -- grouping them in a single genus with no subgeneric groupings -- is not satisfactory. Nor is von Boetticher's arrangement -- with subgenera -- satisfactory. His distribution of the seven species among six subgenera within the genus Mergus is ill advised because:

1. He has erected too many subgenera; with monotypic subgenera it is impossible to show relationships among species.

2. His only subgenus with two species includes two forms that seem to me clearly unrelated.

It is obvious that unless Lophodytes and Mergellus are lumped in a single genus it will be necessary to place the merganser group of species (including australis and squamatus) in a different genus than serrator and octosetaceus; the two groups of species are related only through the common ancestry of Lophodytes and Mergellus. The nomenclatoral alternatives are as follows:

1. Four genera: Mergellus, Lophodytes, Mergus (including australis, squamatus, and merganser), and Prister (including octosetaceus and serrator).

2. Two genera, each with two subgenera:

Mergus (Mergellus) albellus

Mergus (Merganser) australis

Mergus (Merganser) squamatus

Mergus (Merganser) merganser

Lophodytes (Lophodytes) cucullatus

Lophodytes (Prister) octosetaceus

Lophodytes (Prister) serrator

3. One genus and four subgenera:

Mergus (Mergellus) albellus

Mergus (Merganser) australis

Mergus (Merganser) squamatus

Mergus (Merganser) merganser

Mergus (Lophodytes) cucullatus

Mergus (Mergus) octosetaceus

Mergus (Mergus) serrator

The morphological and behavioral differences between serrator and merganser are sufficient to warrant their generic separation. However, it is possible to show all the relationships within the group most conveniently by placing the seven species in a single genus and erecting four subgenera. In a linear classification Mergus (Lophodytes) cucullatus should separate the Mergellus and Merganser group from the Mergus group.

IV. THE EIDERS AND THE HARLEQUIN DUCK

Although I am discussing the eiders and the Harlequin Duck together in this section, I am not sure that the former are very closely related to the latter. The principal reason I am discussing the Harlequin with the eiders rather than with the scoter - golden-eye - merganser group is my conviction that the tracheal bulla is phylogenetically conservative. Although certain features of the plumage of the adult male also favor placing the Harlequin with the eiders, the plumage patterns of the downy young and of the female and immature favor placing it with the scoter - golden-eye - merganser group.

A. Plumage

The plumage patterns of the eiders and the Harlequin were studied from skins representing all the species in the group. I examined downy young of all the species except Histrionicus histrionicus; this species has been well described and figured in the literature.

1. Downy Young

Eiders.-- Except for the head, the plumage patterns of downy young eiders are practically identical. All have light underparts and dark upper parts. The underparts vary from pale tan to pale grayish brown; in some forms (Somateria mollissima dresseri, S. m. borealis, Polysticta stelleri) the throat and upper breast are slightly darker than the rest of the underparts. Dorsally, the plumage

varies from light brown to dark reddish brown and is unrelieved by any light markings. The plumage patterns on the heads of the four species of eiders all have the following in common: 1) the forehead, crown, and nape are dark and match in color the dorsal body plumage; 2) all except Polysticta stelleri have a prominent, pale superciliary; Polysticta has a narrow, light brown superciliary which does not extend anteriorly to the base of the beak. Somateria mollissima and Polysticta have dark plumage below the eye which extends anteriorly to include most of the lore and posteriorly to merge with the dark nape. Ventrally, the dark plumage below the eye grades into the lighter throat plumage. Arctonetta is similar to Somateria mollissima in distribution of the dark plumage below the eye; however, the dark plumage extends above the eye interrupting the superciliary and giving the eye a "spectacled" appearance. Somateria spectabilis is also similar to Somateria mollissima with respect to the dark plumage below the eye except that in S. spectabilis the light throat plumage extends well up on the ventral part of the side of the head.

Harlequin Duck.-- Bent (1925:53-54) states that the downy young Harlequin "is 'bister' or 'Prout's brown' above, including the top of the head down to the level of the eyes, the lores, hind neck, back and rump; the underparts, including the cheeks up to the eyes, are pure white; there is a white spot above and in front of the eye and an

indistinct whitish streak on each scapular region; the front of the wing is margined with white." Witherby et al. (1949:328) describe the pattern on the back of the downy Harlequin as follows: "small brownish-white spot on wing and another on side of back behind wing, both somewhat indistinct; white spot on either side of centre of back above thigh not always well-defined..." From the above descriptions and the figure in Kortright (1942:458), the downy Harlequin seems most similar to downy Melanitta fusca; the two species differ in that the Harlequin has a white spot above the eye and lacks a brown band across the upper breast.

2. Adult Plumage Characters

The following generalizations may be made about the adult plumage characters of the eiders:

1. Several of the most proximal secondaries in both sexes are elongate and sickle-shaped.

2. The head plumage of adult males shows the following characteristics:

a. Sea-green feathers; these vary in amount and distribution among the several species.

b. Short, "plushy" feathers; these also vary in amount and distribution among the several species.

c. Black, v-shaped mark (apex pointing forward on the throat of Somateria spectabilis and Somateria mollissima v-nigra; this mark crops up periodically in other populations of Somateria mollissima, par-

ticularly the nominate race; it has been noted in at least one individual of Arctonetta fischeri. The entire throat of male Polysticta stelleri is black.

3. The lower breast, belly, sides, and flanks are black in males of all eiders except Polysticta; in Arctonetta fischeri upper and lower breast, sides, flanks, and belly are black.

4. The lesser upper secondary coverts of adult males are white; adult males of Polysticta also have white greater upper secondary coverts. The elongate, proximal secondaries are white in Somateria mollissima and Arctonetta fischeri.

5. Adult males of all eiders (and the Harlequin) have a white patch on the lower flank; this patch is small in Histrionicus and Polysticta.

6. All the eiders except Polysticta lack a speculum.

7. Female eiders except Polysticta have black and light brown transversely barred body plumage reminiscent of the female plumage of some species of Anas. Female Polysticta has dark brown plumage faintly barred with black.

The plumage patterns of male and female Harlequin Ducks are very different from those of the eiders. The adult male has a striking pattern of rusty red, gray-blue, black, and white -- not at all reminiscent of the plumage patterns of any of the eiders. The female is uniform gray-brown above; it is paler and mottled whitish on the lower breast and upper belly; it has white markings on the



head which roughly resemble those on the head of juvenile Melanitta fusca and perspicillata. The male Harlequin has an iridescent, dark blue speculum; the female lacks a speculum. Male Polysticta also has an iridescent, dark blue speculum as well as iridescence on the elongated innermost secondaries; the speculum of the female is duller than that of the male.

B. Trachea

I have examined tracheal bullas and complete tracheas of all the species of eiders and the Harlequin Duck.

The tracheal bullas of the eiders and the Harlequin are similar in that each has an inflated left chamber which is bulbous in form and lacks any membrane-covered fenestrae; the right chambers are slightly or not at all inflated and lack membrane-covered fenestrae.

The tracheal bullas of Somateria mollissima, Somateria spectabilis, and Arctonetta fischeri are practically identical in form; they differ from one another only in size. Somateria mollissima v-nigra has the largest tracheal bulla and Arctonetta fischeri the smallest: the tracheal bulla of Somateria spectabilis is intermediate in size. The tracheal bullas of other races of Somateria mollissima are smaller than that of S. m. v-nigra but are slightly larger than that of Somateria spectabilis. The left chamber of the tracheal bullas of each of the above three species is expanded mostly laterally; it is expanded slightly in an anterior direction; medially and ventrally the left

Figure 15. Tracheas and tracheal bullas of the eiders and Harlequin Duck.

a. Somateria spectabilis

b. Arctonetta fischeri

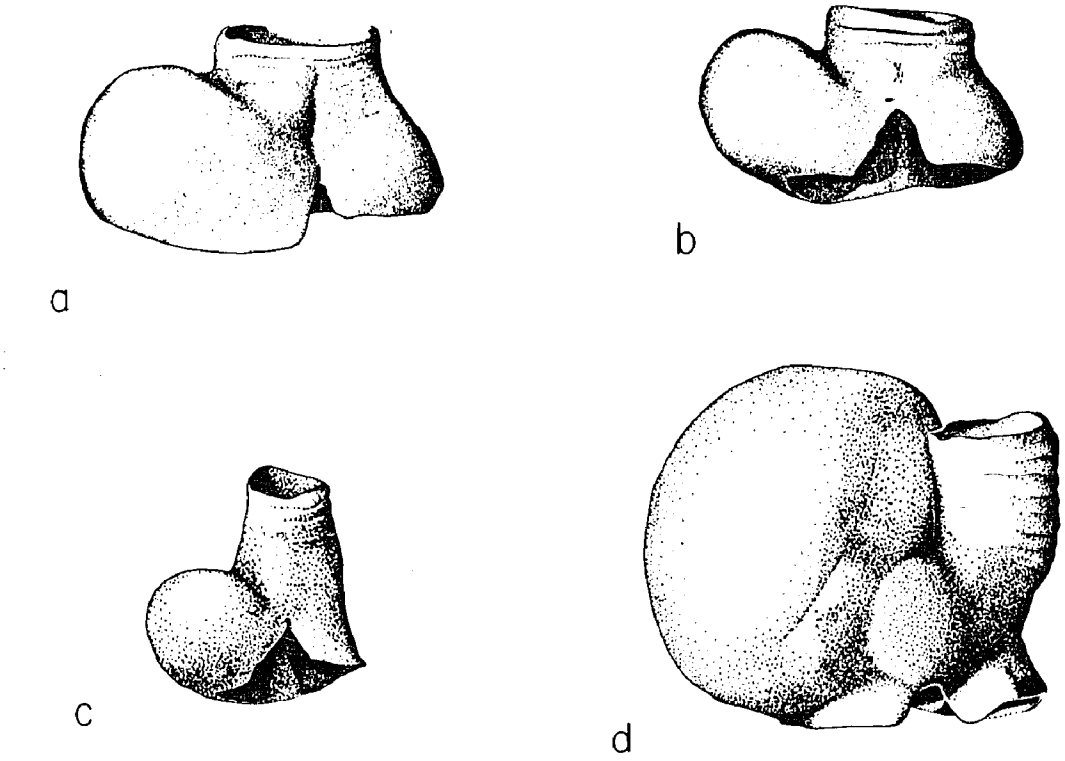
c. Polysticta stelleri

d. Histrionicus histrionicus

e. Somateria spectabilis

f. Polysticta stelleri

g. Histrionicus histrionicus



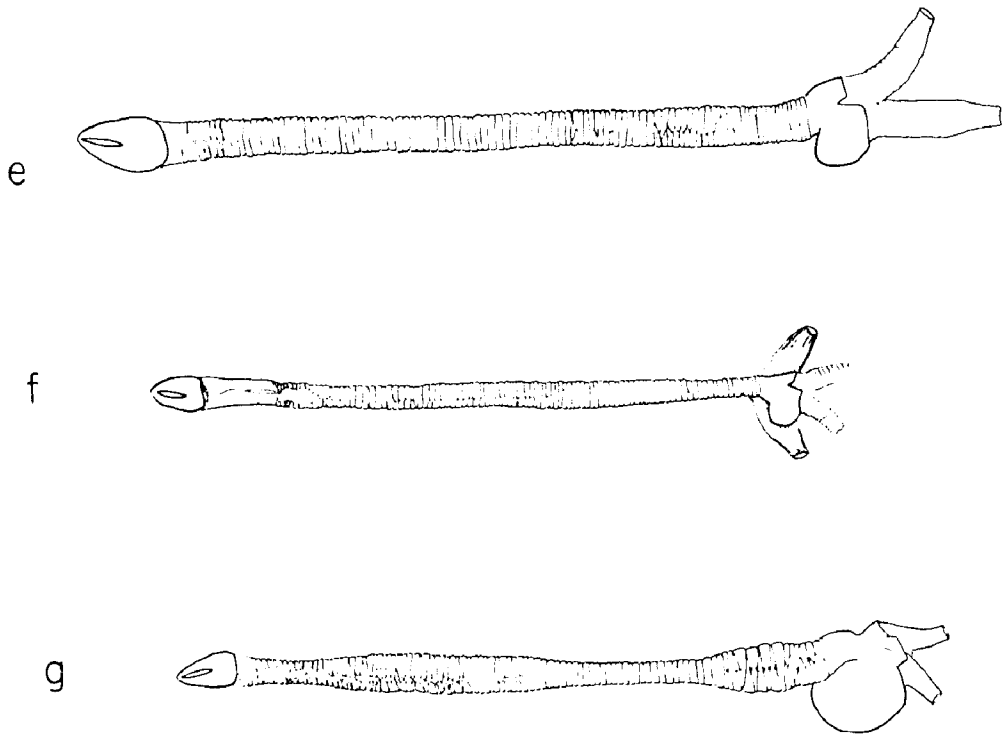


Figure 15.

chamber bulges in a ventral direction. The pessulus is a thin, vertical bar of bone; it is located anteriorly, close to the tracheal aperture of the bulla.

The tracheal bulla of Polysticta stelleri is smaller than those of Somateria and Arctonetta and differs from them as follows:

1. The left chamber is proportionately less expanded.

2. The left chamber has a prominent ventral protuberance at the posterior ventral margin of the bulla between the bronchial apertures; this is not present in Somateria or Arctonetta.

3. The pessulus is wide (antero-posteriorly) in Polysticta; it is very narrow in Somateria and Arctonetta.

4. The shape of the left chamber in Polysticta differs from that of Somateria and Arctonetta.

The tracheal bulla of Histrionicus histrionicus is very different in shape from those of the eiders. The pessulus, instead of being located anteriorly near the tracheal aperture of the bulla, is located posteriorly at the bronchial apertures. The pessulus is wide antero-posteriorly. The left chamber is greatly expanded laterally and anteriorly; it is slightly expanded dorsally and ventrally. Ventrally and close to the midline there is a posteriorly directed expansion of the left chamber. The left chamber is very different in shape from those of the eiders. The tracheal bulla of Histrionicus is strikingly similar to the tracheal bullas of Anas rubripes and Anas

platyrhynchos.

The tracheas of all the eiders except Polysticta are of uniform diameter. The trachea of Polysticta gradually increases in diameter for the most anterior quarter of its length. The bronchi of all the eiders except Polysticta are enlarged, the left one more so than the right; in Arctonetta the left bronchus is only slightly larger than the right. The bronchi of Polysticta are not enlarged and are of equal size. The bronchi of all the eiders are very close to one another. Polysticta is unique in having very much enlarged ypsilo-trachealis muscles.

The trachea of Histrionicus has an enlargement in the most posterior fifth of its length which is twice the diameter of the narrowest part of the trachea. Anterior to the lower enlargement, the trachea has its least diameter; the anterior swelling begins at about the middle of the trachea and continues cephalad to a point a short distance posterior to the larynx where the trachea again becomes reduced in diameter. The bronchi are not enlarged, are of equal size, and are close to one another.

C. Ecology and Diving Habits

1. Nests and Nesting Habitats

The eiders are entirely marine coastal in nesting distribution. They show a wide adaptability (particularly Somateria mollissima) in selection of nest-sites; nests may be placed close to salt water on the marine coast or on islands offshore, or they may be placed a mile or more

inland close to fresh water. Arctonetta, Polysticta, and Somateria spectabilis nest principally in the lowlands, selecting sites in meadows where the vegetation is fairly low and offers little concealment. Somateria mollissima may nest on high ground, in woods, on beaches, or in marshes and other lowland situations. All of the eiders invariably build their nests on the ground; how well such nests are concealed depends to a large extent on local cover conditions.

The Harlequin places its nest on the ground, usually in the shelter of some shrubs or rocks and close to a stream or river.

2. Winter Habitat

Eiders.-- In its winter distribution Steller's Eider is strictly marine. Bent (1925:72) says: "Steller eiders are almost as abundant in their winter resorts about the Aleutian Islands as they are in summer on the Siberian coast. Here they gather in large flocks, associated with king eiders, about the harbors which are free from ice. They resort to the vicinity of sunken ledges and rocky islets where they can obtain their food by diving to moderate depths, although they can dive in deep water if necessary." Nelson (1887:76) says that Steller's Eiders "usually frequented outlying rocky islets and exposed reefs, and fed in the small tide rips....their chosen haunts are along coasts where the water is clear and deep close to shore."

According to Bent (1925:118), "the king eider spends the winter as far north as it can find open water; in southern

Greenland it associates with the northern eider in the open water in the fjords, but probably the greater number spend the winter at sea on the edges of the ice packs or in the open leads." In winter King Eiders frequent submerged ledges, sometimes several miles offshore. Cottam (1939:106) has summarized references on the depths at which King Eiders may feed: "there seems to be convincing evidence that the king eider can and does feed in deeper water and stays under longer than most if not all other ducks, with the possible exception of the old squaw. Hagerup...asserts that it seeks rather deeper water than S. borealis. Norton...found the birds feeding in unusually deep water off the coast of Maine. Sterling...gives record of a bird taken in a gill net 55 feet below the surface, on Lake Erie....Hanna notes that this species can descend to the bottom in 30 fathoms of water, because one that he shot just after it came to the surface of water of this depth had freshly swallowed mollusks in its gullet."

Describing the winter habits of the Common Eider (Somateria mollissima), Bent (1925:87-88) says "Eiders obtain their food...by diving to moderate depths...most of it is found on or about the sunken ledges or submerged reefs off rocky shores....They prefer to feed at low tide when the food supply is only a few fathoms below the surface; they often dive to depths of 6 or 8 fathoms and sometimes 10 fathoms....Even in rough weather these...birds may be seen feeding about the ledges white with breakers..."

Bent (1925:93) says further that "low temperatures have no terrors for them....Even in the roughest winter storms they brave the rigors of the open sea...diving for food among the surf-swept ledges...." Madsen (1954:166) says that the Common Eider probably does not dive much deeper than 10 to 15 meters. Eiders are exclusively marine birds in the winter and occur only infrequently as vagrants on inland waters.

I can find nothing on the winter habitat of the Spectacled Eider; it winters chiefly in the Aleutians and presumably has habitat preferences similar to those of the other eiders.

In winter, the Harlequin Duck has a marine coastal distribution. Bent (1925:56-57) says that they "are fond of feeding in rough water along rocky shores just off the beaches....They are often seen about the rocky bays...in winter, but more often they frequent the outlying rocky islands and ledges." Cottam (1939:81) states that Harlequin Ducks "apparently prefer to feed in rough water that is broken by rocks and surf....Because they feed in shallow water, their dives are of short duration."

3. Diving Habits

Very little is known of the eiders' method of underwater locomotion. There is general agreement that the eiders use their half-spread wings in diving; no one, however, has determined whether or not they use their feet underwater. Bent (1925:89) states that "In diving

the wings are partially opened and used to a limited extent in swimming under water, but the wings are not wholly spread; progress seems to be made mainly by the use of the feet, and there is nothing like the full subaqueous flight practiced by some of the Alcidae." I think that Bent's statement is more a supposition than a statement of pure fact; I know of no published observations on the underwater locomotion of eiders. Phillips (1926:91) says "There is no question but that Eiders use their wings under water, whether or not they are wounded....The Eider uses its wings just as does the Harlequin, held close to the sides and beaten with short jerks, not extended as in aerial flight." It is my personal belief that the eiders depend on their wings for underwater locomotion and do not use their feet at all; however, this will have to be confirmed or denied by actual observation.

When feeding in shallow water, eiders tip up like dabbling ducks. I have observed this behavior many times in Somateria mollissima v-nigra and Arctonetta fischeri; it is undoubtedly also a habit of Somateria spectabilis and possibly of Polysticta stelleri.

The diving habits of the Harlequin Duck in a mountain stream have been described by C. and E. Michael (1922:18-19) as follows: "When feeding...they show no preference as to depth of water. When working up stream along the shore they wade in the shallow water, prying among the stones. Where the water is deeper they tip up in the manner of

Mallard ducks, and where the water is still deeper they dive. They dive in water a foot deep and they dive in water six feet deep, always going down where there is a gravelly bottom....To leave the surface of the water they use their wiry tails as a spring to make the plunge and as they go down both wings and feet are used as a medium of propulsion. When once on the gravelly bottom the wings are closed, the head is held low, and the progress is made against the current, as they walk along poking amongst the stones....The head is held down by physical strength. The current against the angle of the body throws pressure on the feet and enables the bird to maintain its position without swimming. When the current comes with just the right speed the bird may stand still, but in lesser currents the bird must move forward."

4. Food Habits

There is good reason to believe that all of the eiders take large percentages of plant foods while on the breeding grounds and take predominantly animal foods when away from the breeding grounds. There are too few data from adult birds taken on the breeding grounds to characterize adequately their feeding habits during that season.

Cottam (1939:93, 104, 113) has described the stomach contents of downy young eiders as follows: Polysticta stelleri about 40 per cent plant food, Somateria mollissima v-nigra about 70 per cent plant food, and Arctonetta fischeri

about 45 per cent plant food. The diets of downy young of the scoters, Old-squaw, golden-eyes, and Buffle-head contained no more than 25 per cent plant material; downy young of most of the species Cottam (1939) studied had subsisted on less than 20 per cent plant food.

The winter (or marine) diets of the eiders (except Polysticta) are very similar to those of the scoters; the winter diet of Polysticta seems to be roughly similar to that of Clangula. According to Cottam (1939:90), the diet of Steller's Eider contains approximately 60 per cent crustacea and insects and 20 per cent molluscs. Cottam, however, has not distinguished between birds taken on and birds taken away from the breeding grounds; the percentages of different kinds of food are therefore misleading. Phillips (1926:70) lists the stomach contents of 46 marine-taken birds as comprising approximately 60 per cent crustaceans and 40 per cent molluscs. Madsen (1954:203) describes the marine diet of Clangula hyemalis as consisting of about 50 per cent molluscs and 30 per cent crustaceans.

Phillips (1926:93), describing the winter food of Somateria mollissima, says that it "is similar to that of the Scoters; if anything it is coarser, that is, larger objects are taken. In most places Eiders are almost dependent on mussel-banks, while sea-clams, scallops, razor-fish and snails are important items. They seem to pick up more crabs than other sea ducks do...." Madsen (1954:177)

states that "the foods...taken by the Eider, blue mussels, crabs, and sea-stars, are immobile or...slow-moving species which live on the bottom and...are easily collected, the sea-stars...can be directly picked up, whereas blue mussels may have to be detached from stones....Other species eaten by the Eider...may have to be ploughed up by the beak...." Madsen (1954:173) found that about 67 per cent of the food of Somateria mollissima in marine habitats comprised molluscs; about 17 per cent comprised crustaceans, and about 15 per cent comprised echinoderms.

Describing the food habits of Somateria spectabilis, Phillips (1926:124) says "the food habits of the duck are well illustrated in the Pribilof Island area by a series of forty-four well-filled stomachs studied by W. L. McAtee. The nature of the food is very like that found in the Common Pacific Eider for the same region...the King Eider takes fewer molluscs and a much lower percentage of star-fishes, making up for it by a greater consumption of bar-nacles and fishes. The proportions were as follows: mollusks 34.36%; crustaceans 28.2%; sea-urchins, 9.54%; starfishes, 2.59%; and algae, 9.88%....There were other items of food of lesser importance....The favorite animal food was the common blue mussel...."

The food habits of Arctonetta fischeri seem to be roughly similar to those of the other large eiders. Cottam (1939:111) says "mollusks supplied the largest volume of animal food for the spectacled eider. Bivalves...(34.05

percent) predominated, and more than half of these were razor clams (19 percent), which furnished 57 percent of the entire food of eight birds taken in May....It is probable that the consumption of mollusks would be even greater in winter, because winter birds do more of their feeding in the ocean or salt-water bays, where...the food would show a marked reduction in vegetable and insect material and a corresponding increase in marine invertebrates, such as mollusks and crustaceans."

Cottam (1939:81) describes the diet of the Harlequin Duck as follows: "during both summer and winter, the birds subsist principally upon an animal diet (98.32 percent) made up mainly of crustaceans (57.13 percent)...and mollusks (24.68 percent)....chitons, which appear as the dominant molluscan food...are found securely attached by suction to rocky coastal surfaces."

D. Skeletal Proportions

1. Specimens

My study of the skeletal proportions of the eiders and the Harlequin Duck was based on 50 skeletons, representing all the genera and species in the group. Specimens (all males) measured were:

Somateria mollissima v-nigra	6
Somateria mollissima dresseri	8
Somateria spectabilis	6
Arctonetta fischeri	18

Species	Humerus			Ulna			Manus			Wing		
	Mean	σ	N	Mean	σ	N	Mean	σ	N	Mean	σ	N
Somateria m. v-nigra	116.6	3.6	6	103.4	2.2	6	122.6	4.0	6	342.6	9.7	6
Somateria m. dresseri	107.7	1.9	8	95.1	2.2	7	114.6	2.9	8	318.0	6.5	7
Somateria spectabilis	99.2	2.4	6	87.9	2.3	6	107.3	2.5	6	294.4	6.8	6
Arctonetta fischeri	95.4	1.7	18	83.9	1.4	18	100.4	2.0	18	280.0	4.4	18
Polysticta stelleri	71.7	1.0	11	64.4	0.8	11	81.6	1.6	11	217.7	2.8	11
Histrionicus histrionicus	66.3	-	1	57.8	-	1	73.3	-	1	197.4	-	1

Table 15. Mean greatest lengths of humerus, ulna, manus, and wing (all male specimens). (σ, standard deviation; N, number of specimens measured.)

Species	Femur			Tibiotarsus			Tarsometatarsus			Digit III		
	Mean	σ	N	Mean	σ	N	Mean	σ	N	Mean	σ	N
Somateria m. v-nigra	67.3	2.9	6	105.6	4.3	6	54.6	2.2	6	65.8	3.1	6
Somateria m. dresseri	63.2	1.9	8	101.2	2.9	8	53.5	0.9	8	65.7	1.5	8
Somateria spectabilis	56.1	1.5	6	89.4	2.7	6	46.2	1.8	6	56.4	6.0	6
Arctonetta fischeri	57.4	1.1	16	91.1	1.4	18	47.4	1.0	18	54.0	1.7	18
Polysticta stelleri	46.1	1.0	11	72.1	1.2	11	39.3	0.7	11	50.0	1.0	11
Histrionicus histrionicus	42.0	-	1	69.5	-	1	38.1	-	1	47.1	-	1

Table 16. Mean greatest lengths of femur, tibiotarsus, tarsometatarsus, and digit III (all male specimens). (σ, standard deviation; N, number of specimens measured.)

Species	Leg			Weight			Pollex			Sternum + Coracoid		
	Mean	σ	N	Mean	σ	N	Mean	σ	N	Mean	σ	N
Somateria m. v-nigra	293.4	11.8	6	2320	-	3	27.5	1.2	6	172.6	6.7	6
Somateria m. dresseri	283.6	5.7	8	2105	-	1	25.8	0.8	8	160.4	2.5	8
Somateria spectabilis	248.1	7.3	6	1715	-	1	23.4	0.6	6	152.3	3.6	6
Arctonetta fischeri	250.2	4.0	16	1560	-	1	22.5	0.7	16	149.3	4.0	18
Polysticta stelleri	207.0	4.0	11	871	-	1	18.4	0.6	11	120.8	2.4	11
Histrionicus histrionicus	196.7	-	1	675	-	7	15.8	-	1	115.9	-	1

Table 17. Mean greatest lengths of leg, pollex, and sternum + coracoid; mean weight (all male specimens). (σ, standard deviation; N, number of specimens measured.)

Species	Trunk Length			Synsacrum Length			Synsacrum Width			Sternum Width		
	Mean	σ	N	Mean	σ	N	Mean	σ	N	Mean	σ	N
Somateria m. v-nigra	114.1	2.3	6	45.7	2.1	6	29.5	1.2	6	60.2	1.5	6
Somateria m. dresseri	109.6	5.5	8	43.8	4.0	8	28.5	1.3	8	58.9	2.2	8
Somateria spectabilis	103.4	1.4	5	44.2	2.4	6	24.1	3.1	6	50.7	1.9	6
Arctonetta fischeri	96.2	2.8	18	39.7	2.4	18	24.2	0.9	18	52.9	2.0	18
Polysticta stelleri	77.8	2.0	11	30.7	1.1	11	21.3	0.9	10	39.8	1.3	11
Histrionicus histrionicus	67.6	-	1	25.8	-	1	20.0	-	1	37.0	-	1

Table 18. Mean lengths of trunk and synsacrum; mean widths of sternum and synsacrum (all male specimens). (σ, standard deviation; N, number of specimens measured.)

Polysticta stelleri	11
Histrionicus histrionicus	1

2. Wing

I determined the relative sizes of the distal elements of the wing (ulna, pollex, manus) by expressing the mean length of each of them as a percentage of mean humerus length. The interspecific variation of these three sets of ratios is illustrated in Figure 10. Except for variations in the manus:humerus ratios, the large eiders (*Somateria* and *Arctonetta*) and the Harlequin are very similar in wing proportions. *Histrionicus* has a relatively longer manus than *Somateria* or *Arctonetta*; *Somateria spectabilis* has a manus which is longer than those of the other large eiders but shorter than that of *Histrionicus*. *Polysticta* has wing elements which, expressed as percentages of mean humerus length, are consistently larger than those of any of the other eiders or the Harlequin.

A comparison of the relative lengths of the wing elements of the eiders and Harlequin with those of the members of the scoter - golden-eye - merganser group reveals that the ulna is relatively longer in those birds that use their wings in diving. I discussed this matter in Chapter III, where I pointed out that the differences between the species with respect to ulna length are slight, and further, that length of the ulna in *Bucephala islandica* (which does not use its wings under water) exceeds the ulna

Species	Ulna	Manus	Pollex	Femur	Tibio-tarsus	Tarsometa-tarsus	Digit III
Somateria v-nigra	88.7	105.1	23.6	57.7	90.5	46.9	56.5
Somateria m. dresseri	88.5	106.4	24.0	58.8	94.2	49.7	61.1
Somateria spectabilis	88.5	108.2	23.6	56.6	90.1	46.6	56.8
Arctonetta fischeri	88.0	105.4	23.6	60.2	95.6	49.6	56.6
Polysticta stelleri	89.7	114.0	25.6	64.4	100.7	54.8	69.7
Histrionicus	87.2	110.6	23.8	63.4	104.9	57.5	71.2

Table 19. Mean lengths of elements (ulna, manus, pollex, femur, tibiotarsus, tarsometatarsus, digit III) expressed as percentages of mean humerus length.

length of Arctonetta fischeri (which does use its wings under water). The adaptive significance (with respect to underwater locomotion) of variations in length of ulna requires further study. The fact that the skeletal proportions are probably strongly limited by the adaptation to aerial flight makes the problem especially difficult.

Variations in the relative lengths of pollex and manus are apparently not correlated with variations in underwater locomotor habits.

3. Trunk

The eiders and Harlequin have trunk lengths (expressed as percentages of mean humerus length) which are consistently larger than those of the scoters and (except for Polysticta) considerably smaller than those of the "true" mergansers. Relative sternum plus coracoid length is smaller in Arctonetta and Somateria than in all Mergini but the scoters; Polysticta has a relative sternum plus coracoid length which is greater than that of Mergus serrator. The sternum plus coracoid length of Histrionicus is greater than those of Somateria and Arctonetta but much less than that of Polysticta (see Figure 11).

Sternum width in the eiders and Harlequin varies from 51.1 (in Somateria spectabilis) to 55.8 per cent of humerus length (in Histrionicus histrionicus). The scoters and Old-squaw vary in this measurement from 48.3 (in Oidemia nigra) to 54.5 per cent of humerus length. When

Species	Trunk Length	Synsacrum Width	Sternum Width	Anterior Keel Extent	Sternum + Coracoid	Wing Length
Somateria v-nigra	98.0	25.3	51.6	16.4	148.0	117.0
Somateria m. dresseri	102.0	26.4	54.6	15.5	159.0	112.1
Somateria spectabilis	104.1	24.3	51.1	16.7	153.8	118.7
Arctonetta fischeri	100.9	25.4	55.5	14.9	156.9	111.1
Polysticta stelleri	108.3	29.7	55.5	14.0	168.2	105.0
Histrionicus	102.0	30.2	55.8	15.8	159.0	100.3

Table 20. Mean measurements of elements (trunk length, synsacrum width, sternum width, anterior keel extent, sternum + coracoid length) expressed as percentages of mean humerus length; mean wing length expressed as a percentage of mean leg length.

trunk length, sternum plus coracoid length, and sternum width are considered together, it seems clear that the scoters, and Somateria and Arctonetta have very similar trunk proportions; Histrionicus seems most similar to Bucephala in these proportions, while Polysticta seems most similar to Clangula.

There is, except for Clangula hyemalis, a correlation between the magnitude of anterior keel extent expressed as a percentage of mean humerus length and the method of underwater locomotion. All the eiders and the Harlequin have small anterior keel extents; that of Polysticta is smallest. Each of the scoters likewise has a small anterior keel extent. The anterior keel extent of the Old-squaw is almost as large as that of the Common Golden-eye (see Figure 11).

In the scoter - golden-eye - merganser group, the "true" mergansers and the scoters have relatively narrow synsacra (18.0 to 23.0 per cent of humerus length); the Old-squaw, golden-eyes, Smew, and Hooded Merganser have relatively wide synsacra (25.4 to 30.2 per cent of humerus length). Synsacrum width seems to be correlated with swift underwater locomotion where propulsion is supplied principally by the feet. The eiders and the Harlequin have wide synsacra (24.3 to 30.2 per cent of humerus length).

4. Leg

The leg elements of the eiders show considerable interspecific variation when expressed as percentages of humerus

length. Femur length ranges from 56.6 to 60.2 per cent of humerus length in Somateria and Arctonetta; the femur length of Polysticta is 64.4 per cent of humerus length, while that of Histrionicus is 63.4 per cent of humerus length. Femur length in the "true" mergansers ranges from 53.8 to 57.0 per cent of humerus length; femur length in the scoters varies from 56.8 to 59.7 per cent of humerus length; in Bucephala femur length varies from 60.7 to 62.5 per cent of humerus length. Somateria and Arctonetta and the scoters are roughly similar in relative length of femur; however, Somateria and Arctonetta have wide synsacra (24.3 to 26.4 per cent of humerus length), while the scoters have narrow ones (18.0 to 22.4 per cent of humerus length).

Tibiotarsus length in Somateria and Arctonetta varies from smaller than those of the scoters and "true" mergansers to larger than those of the mergansers and two of the scoters (see Figure 13). However, the ratio of femur length to tibiotarsus length is similar in all the eiders, the Harlequin, the scoters, and the Old-squaw (see Figure 12). Tarsus length and digit III length are relatively much less in Somateria and Arctonetta than in any of the other species of Mergini.

Polysticta and Histrionicus are both consistently much larger than Somateria and Arctonetta in relative length of the leg elements. This leads me to suspect that some of the differences shown by these two species are attributable to reduced humerus length. The extreme

example of humerus reduction in the Mergini is Mergus australis; in this species the ratio of wing length to leg length is 94.4 per cent and the distal wing elements are considerably shorter than in the related species of mergansers. I suspect that Bucephala albeola has a reduced humerus length; although the distal wing elements of this species do not show excessive reduction, they are in general slightly shorter than in the related species; the wing length:leg length ratio in Bucephala albeola is 100.1 per cent. Polysticta and Histrionicus have wing length:leg length ratios respectively of 105.0 and 100.3 per cent; neither of the species shows any reduction of the distal wing elements (which one would expect in cases of humerus reduction) and the manus of each of the species is much longer than in Somateria and Arctonetta. I am unable to account for the extreme differences among the skeletal proportions of Polysticta and Histrionicus and the big eiders; I do not believe that humerus reduction alone can account for all the differences.

E. Relationships

The structure of the trachea and tracheal bulla and the plumage patterns of adult and young eiders lead me to believe that these birds are not closely related to the scoters, golden-eyes, and mergansers. The structure of the trachea and tracheal bulla of the eiders and the dabbling ducks (Anatini) are very similar: likewise, the

plumage patterns of the females of both groups have much in common. I believe that the eiders are much more closely related to the dabbling ducks than to the scoters, goldeneyes, and mergansers. The diets of downy young eiders consist of from 40 to 70 per cent plant food; presumably the adults on the breeding grounds also consume a great deal of plant material. Although more information is needed on the summer (breeding grounds) diets of the eiders, their summer feeding habits are reminiscent of those of the dabbling ducks, which depend largely on plants as a source of food. Furthermore, the eiders' method of feeding on the breeding grounds (tipping up) is very similar to that of the dabbling ducks.

In their locomotor adaptations, the eiders (particularly Somateria and Arctonetta) have much in common with the scoters; the feeding habits and winter ecological distributions of the two groups of species are very similar. There are, however, a number of striking differences between these two groups of diving birds.

I have been unable to learn whether or not eiders use their feet in addition to their wings for underwater locomotion, but a number of structural and behavioral features of the eiders leads me to believe that they do not depend on their feet for propulsion under water.

The femora of eiders are slightly or not all flexed at their distal ends; the scar which serves as the origin of the femoral head of the gastrocnemius is very short.

The femora of non-diving anatids such as geese and dabbling ducks are not flexed and have very short scars for the origin of the femoral head of the gastrocnemius. The femora of diving ducks which depend largely on their hindlimbs for underwater locomotion are strongly flexed and the scar for the origin of the external head of the gastrocnemius is very long. Loons, grebes, golden-eyes, mergansers, Old-squaw, and scoters all have a strongly flexed femur with a long scar for the origin of the femoral head of the gastrocnemius; alcids and penguins use their wings and not their feet for underwater locomotion and have a femur which is not flexed and which bears a short gastrocnemial scar.

The eiders and scoters are quite similar with respect to the skeletal proportions which seem to be correlated with use of the wings as a means of underwater propulsion. The anterior extent of the keel is small and the ulna long in both groups of species. The scoters and Somateria and Arctonetta have very similar trunk proportions.

The scoters and eiders are very different in several skeletal proportions which appear to be related to use of the hindlimb for underwater propulsion. The scoters have narrow synsacra, whereas those of the eiders are wide; the range of variation in femur length is about the same in the scoters and the eiders. The ratio of femur length to tibiotarsus length is similar in the eiders and the scoters. Finally, digit III is very long (69.5 to 71.6 per cent of humerus length) in the scoters, and very short in the eiders

(56.5 to 61.1 per cent of humerus length). These facts suggest but do not prove that the eiders do not use their feet in addition to their wings as a means of underwater propulsion. The structural characteristics of the eiders strongly indicate that they rely mostly on their wings for underwater propulsion whether or not the feet are used.

I believe that the eiders and the scoters are the products of convergent evolution. I judge that the scoters began their adaptive evolution in an inland, shallow, fresh-water environment (see Chapter III). The eiders, on the other hand, probably developed from a group of dabbling ducks (Anatini) that invaded the marine coastal habitat. There, the ancestral eiders presumably developed feeding habits in which animal material played an increasingly important role. Development of the diving adaptation enabled these birds to utilize food resources in deeper water. Most dabbling ducks dive occasionally; in diving, they use their wings as the means of propulsion. The marine coastal nesting distribution of the eiders and their dependence on the wings as the most important means of underwater locomotion lead me to believe that they underwent the early stages of their adaptive evolution in that environment.

The relationships and possible adaptive evolution of the Harlequin Duck require further study. I feel that the affinities of this species will be clarified when more is learned about other groups of ducks.

F. Genera

1. Eiders

Delacour and Mayr (1945:33) place the four species of eiders in the genus Somateria on the ground that differences in plumage patterns and bill shape do not constitute valid generic criteria. I agree with those authors that Arctonetta should be placed in Somateria for the following reasons:

1. The structure of the trachea and tracheal bulla of Arctonetta is practically indistinguishable from that of Somateria.

2. The plumage pattern of downy young Arctonetta differs from that of Somateria only in a slight modification of the pattern around the eye.

3. The differences in plumage patterns of adult male Arctonetta and Somateria are principally ones of distribution of black on the ventral parts and of pattern on the head; in most other particulars the plumage patterns are very similar.

4. The plumage patterns of the females are very similar, the major peculiarity of Arctonetta being the modified pattern around the eye.

5. The skeletal proportions of Arctonetta and Somateria are very similar.

6. An adult male specimen of Arctonetta (Colorado Museum of Natural History No. 8663) has the black gular "V" characteristic of Somateria spectabilis and Somateria mollissima v-nigra. This V-shaped throat marking has

appeared frequently in races of Somateria mollissima other than v-nigra. Its occurrence suggests that all the forms in which it appears have a close genetic affinity.

For the following reasons I consider that Polysticta should not be merged with Somateria:

1. The structure of the tracheal bulla and the associated ypsilo-trachealis muscles of Polysticta differs from that of Somateria.

2. The plumage patterns of adult Polysticta are very different from those of Somateria. The presence of a speculum in both sexes of Polysticta sets that species apart from the species of Somateria.

3. The skeletal proportions of Polysticta are strikingly different from those of Somateria (see Figures 10, 11, 12, and 13).

I suspect that further study may reveal that Polysticta developed from the ancestral anatine stock independent of Somateria.

V. CONCLUSIONS

I am basing my conclusions on the relationship of the scoters, Old-squaw, golden-eyes, and mergansers mainly on three morphological characters: 1) structure of trachea and tracheal bulla, 2) plumage patterns of downy young, and 3) plumage patterns of adults (particularly the pattern on the secondaries). In terms of these three sets of characters the eiders have no relationship with the scoter - golden-eye - merganser group, and the relationship of the Harlequin with either group is not clear. The data on skeletal proportions do not supply unequivocal evidence for the monophyletic origin of the scoter - golden-eye - merganser group nor do they offer convincing proof that the eiders are or are not related to the scoters, golden-eyes, and mergansers. However, taken in conjunction with evidence from the structure of the trachea and tracheal bulla and with evidence from plumage patterns, it is possible to interpret the data on skeletal proportions in a way that sheds considerable light on the adaptive evolution that may have taken place within the scoter - golden-eye - merganser group and within the eider group. This interpretation is further clarified when observations on the diving, feeding, and nesting habits of the species are considered.

The Tribe "Mergini" does not appear to be taxonomically valid. My evidence indicates that it consists of two unrelated groups of birds which have independently evolved similar adaptations.

I feel that the relationships of the species within the scoter - golden-eye - merganser groups are as follows:

1. The scoters probably most closely resemble the ancestral stock of the group. The three species of scoters should be placed, as Delacour and Mayr have suggested, in a single genus, Melanitta.

2. The Old-squaw (Clangula) appears to be more closely related to the scoters (Melanitta) than to the golden-eyes (Bucephala) or mergansers (Mergus).

3. The golden-eyes and mergansers are, as Delacour and Mayr pointed out, very closely related to one another. The Smew and Hooded Merganser are structurally and adaptively intermediate between the two groups.

4. The golden-eyes and Buffle-head do not differ sufficiently to be placed in separate genera.

5. The Smew and Hooded Merganser differ in many ways from the "true" mergansers (Mergus in the restricted sense). However, the relationships of the species would be obscured by retaining the genera Mergellus (the Smew) and Lophodytes (the Hooded Merganser); I agree with Delacour and Mayr that the seven species of mergansers should be placed in the genus Mergus. I advocate recognizing four subgenera of mergansers on the ground that the differences among the species and their relationships with one another warrant some sort of nomenclatoral interpretation.

The eiders (Somateria and Polysticta) seem to be more closely related to the dabbling ducks (Anatini) than to

the scoter - golden-eye - merganser group. I agree with Delacour and Mayr that Arctonetta should be placed in Somateria; however, I feel that Polysticta differs sufficiently from Somateria to warrant its retention as a good genus.

The relationships of the Harlequin Duck (Histrionicus) are not clear; further study of other groups of ducks may clarify the affinities of this species.

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